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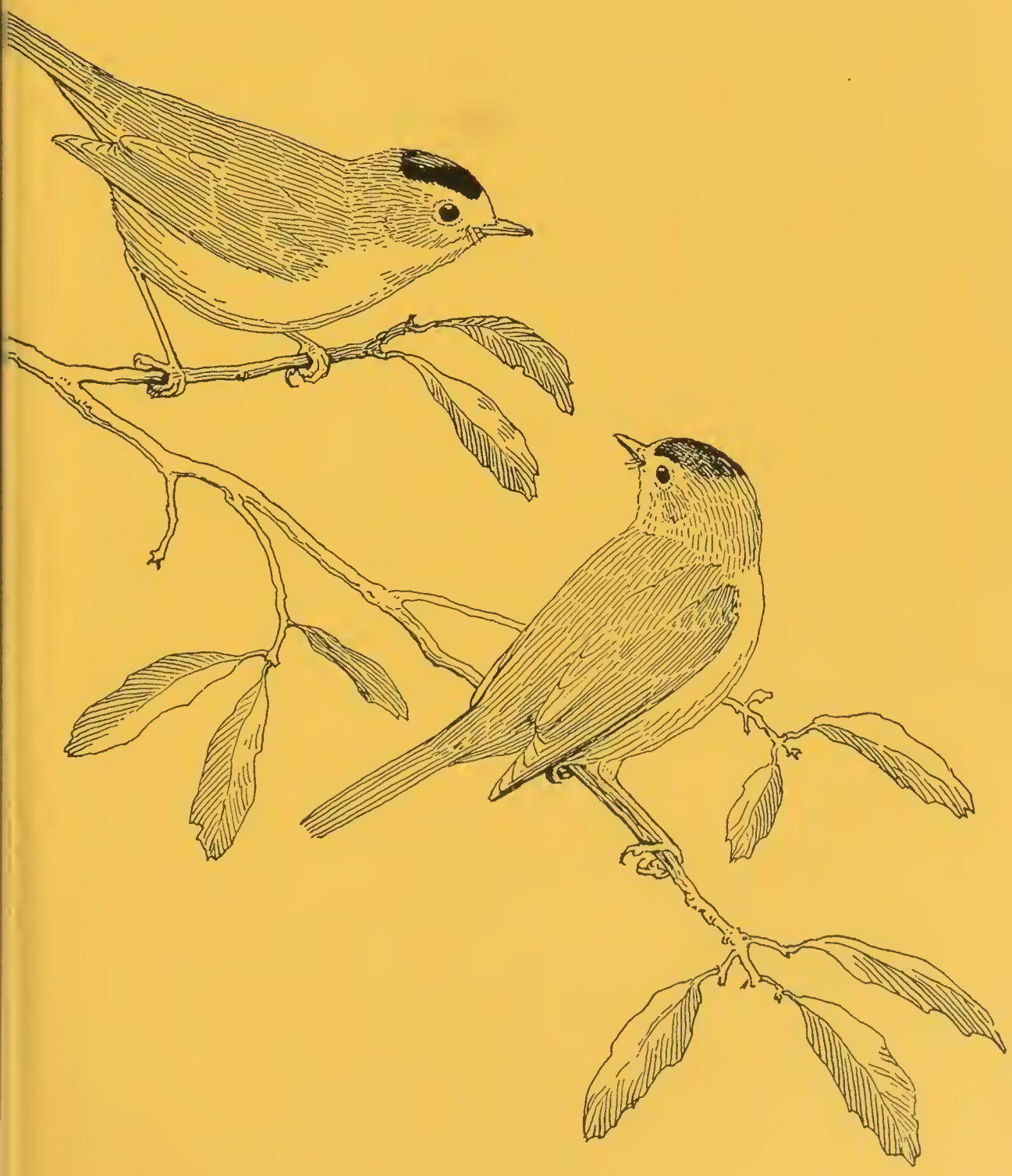
The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 108, NO. 1 MARCH 1996 PAGES 1–204

(ISSN 0043-5643)



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THE WILSON BULLETIN
(ISSN 0043-5643)

THE WILSON BULLETIN (ISSN 0043-5643) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th Street, Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Second-class postage paid at Lawrence, KS. POSTMASTER: Send address changes to THE WILSON BULLETIN, P.O. Box 1897, Lawrence, KS 66044-8897.

Back issues or single copies are available for $12.00 each. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

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Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

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Frontispieee. The Chiribiquete Emerald, *Clulorostilbon olivaresi*. Male (above right) perched on branch of *Tepuianthus savannarum*; female (below left) feeding from flowers of *Decagonocarpus cornutum*, on a mesa of the Sierra de Chiribiquete, southeastern Colombia.

THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Society

VOL. 108, NO. 1 MARCH 1996 PAGES 1–204

Wilson Bull., 108(1), 1996, pp. 1–27

A NEW SPECIES OF EMERALD HUMMINGBIRD (TROCHILIDAE, *CHLOROSTILBON*) FROM THE SIERRA DE CHIRIBIQUETE, SOUTHEASTERN COLOMBIA, WITH A REVIEW OF THE *C. MELLISUGUS* COMPLEX

F. GARY STILES[1]

ABSTRACT.—The Chiribiquete Emerald (*Chlorostilbon olivaresi* sp. nov.) is described from the Sierra de Chiribiquete, an isolated range of table-top mountains rising from the flat Amazonian lowlands of the Departments of Guaviare and Caquetá, SE Colombia. This hummingbird is a common inhabitant of the edaphic scrub and adjacent forests of the middle and upper levels of the Sierra, but evidently does not occur in the surrounding lowlands. In its morphology, the new species shows closer affinities with *C. gibsoni* of the Magdalena Valley than with the adjacent cis-Andean populations of *C. mellisugus*, but it is much larger than all related forms. The Chiribiquete Emerald probably originated through the dispersal of *gibsoni*-type birds to the Sierra during a dry period of the Pliocene or early Pleistocene, perhaps in conjunction with hybridization with the local form of *mellisugus*; large body size probably evolved subsequently in the population as a response to its peculiar, insular habitat. Variation in the *Chlorostilbon mellisugus* complex in NW South America is described and analyzed, and I conclude that the various forms are best treated as comprising a single superspecies; *melanorhynchus* (including *punilus*) of western Colombia and western Ecuador is sufficiently distinct from the adjacent *assimilis* and *gibsoni*, as well as from the eastern forms of *C. mellisugus* to deserve (allo)species rank, and I suggest for it the English name of West Andean Emerald. I recommend recognition of the following allospecies (from north to south): *auriceps, forficatus, canivetii, assimilis, melanorhynchus, gibsoni, olivaresi,* and *mellisugus*. *Received 16 Feb. 1995, accepted 10 June 1995.*

ABSTRACTO.—Se describe *Chlorostilbon olivaresi* sp. nov. de la Sierra de Chiribiquete, una serie aislada de mesetas en la planicie amazónica de los Departamentos del Guaviare y del Caquetá, SE Colombia. Este colibrí es común en las sabanas casmófitas y los bosques aledañas de la parte media y superior de la Sierra, pero evidentemente no ocurre en los bosques basales circundantes. Por sus caracteres morfológicos, *C. olivaresi* probablemente tiene más afinidad con *C. gibsoni* del Valle del Magdalena, que con las formas cisandinas

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vecinas de *C. mellisugus*, pero es un ave mucho más grande que cualquier forma de estas especies. La población de *C. olivaresi* posiblemente originó a través de la dispersión de un(os) individuo(s) del tipo *gibsoni* a la Sierra durante un período seco del Pliocenò o Pleistoceno temprano, tal vez incluyendo hibridización con la forma local de *mellisugus*; subsecuentemente, el tamaño corporal grande evolucionó en esta población en respuesta a su hábitat peculiar y aislado. Se describen y se analizan los patrones de variación en el complejo de *Chlorostilbon mellisugus* en el NO de Suramérica, y se concluye que *melanorhynchus* (incluyendo a *pumilus*) del O de Colombia y Ecuador es suficientemente distinta de *gibsoni* y *assimilis*, las formas adyacentes, como para ser considerado como una (alo)especie. Recomiendo que el complejo de *C. mellisugus* se considere como una sola superespecie, constituida por las aloespecies (de norte a sur) *auriceps, forficatus, canivetii, assimilis, melanorhynchus, olivaresi,* y *mellisugus.*

The small hummingbirds of the genus *Chlorostilbon* are widespread in the Neotropics from central México to northern Argentina and the West Indies. The genus is quite uniform in coloration: males of all species have flashing green underparts, while females are pale gray below, nearly always with a distinctive facial pattern and dusky malar auricular area bordered above by a white postocular stripe. Several species are easily distinguished by the distinctive form and color of the rectrices of the males (e.g., *poortmanni, alice, stenura*), very bronzy or coppery coloration (*russatus*), or extensively red bills (*aureoventris*). However, a number of mostly or entirely allopatric forms in which the males have blue, more or less forked tails, have long been a source of taxonomic confusion. These forms, which collectively might be called the "*mellisugus* complex", cover most of the range of the genus from México to Bolivia and eastern Brazil. Variation among them involves bill color and, in males, the presence or absence of a glittering crown, the depth of the tail fork, the shape of the outer rectrices, and the color of the underparts and, in females, the shape of the rectrices and the amount of gray in the outer rectrices (cf Zimmer 1950). Geographic variation in these characters presents something of a mosaic pattern, with similar forms often separated by others of rather different appearance, making the determination of species limits controversial. The discovery of a new form in the *C. mellisugus* complex, here described as a new (allo)species, makes it desirable to review the patterns of geographic variation in this complex in northwestern South America, and to reevaluate the relationships among the various members of the complex as a whole in the light of recent studies.

The avifauna of Colombia has received at least as much attention from ornithologists, both native and foreign, as has that of any large South American country. The birds of Colombia have been comprehensively monographed no less than three times (Chapman 1917, Meyer de Schauensee 1948–1952, Hilty and Brown 1986). Nevertheless, many parts of Colombia

have been visited only briefly or sporadically by ornithologists, and a number of areas remain ornithologically unexplored. Until very recently, one such area was the Sierra de Chiribiquete, a small, isolated mountain range in the Departments of Guaviare and Caquetá. Because of its topographic uniqueness and pristine character, this area had been set aside as the Parque Nacional Natural Chiribiquete in September 1989, but aside from a visit by botanist Richard E. Schultes in 1943–1944, the Sierra remained biologically unexplored until the present decade. The only previous ornithological collections from this entire region of Colombia were made by H. Romero for the Instituto de Ciencias Naturales of the Universidad Nacional de Colombia at Araracuara, over 100 km S of the Sierra de Chiribiquete on the Río Caquetá, in August–September 1977.

Between December 1990 and December 1992, three expeditions to the Sierra de Chiribiquete were organized by the Agencia Española de Cooperación Internacional, the Instituto de Ciencias Naturales, and the Instituto de Recursos Naturales Renovables (INDERENA) of the Colombian government. The first two expeditions, in December 1990 and August 1991, were devoted to botanical, archaeological, and geological studies. During the first expedition, the Colombian botanists P. Palacios and P. Franco obtained a specimen of an unusual hummingbird (the only bird specimen taken) that I was unable to identify: it appeared to be the male of an undescribed form of *Chlorostilbon,* notable for its very large size, but its rather rough preparation made precise comparisons with other material difficult.

I obtained additional material of this hummingbird during the third expedition (18 November–2 December 1992). With J. L. Tellería and M. Díaz of the Universidad Complutense of Madrid, I observed and collected birds in the vicinity of the expedition's base camp in the northern part of the Sierra at 0°56′N, 72°42′W at the site called "el Valle de los Menhires" (Valley of the Monoliths) by Estrada and Fuertes (1993). Seven specimens (3 males, 4 females) of the *Chlorostilbon* were collected and eight others measured and released; all specimens are housed in the collection of the Instituto de Ciencias Naturales. On the basis of this sample, I here describe this hummingbird as

Chlorostilbon olivaresi, sp. nov.

CHIRIBIQUETE EMERALD

HOLOTYPE.—Adult male, no. 31266 of the ornithological collection of the Instituto de Ciencias Naturales (original number FGS 2941), collected on 24 November 1992 in the Valle de los Menhires, elev. 570m, Sierra de Chiribiquete, Dcpto. del Caqueta, Colombia (0°56′N, 72°42′W) by F. G. Stiles, J. L. Tellería, and M. Díaz.

PARATYPES.—One adult male (ICN 31252, orig. no. FGS 2927) and one sub-adult male (ICN 31253, orig. no. FGS 2928) taken on 21 Nov. 1992 and three adult females (ICN

31244, 31245, and 31254, orig. nos. FGS 2915, 2916, 2929) and one subadult female (ICN 31243, orig. no. FGS 2914), taken on 19 and 24 Nov. 1992, all at the type locality.

DIAGNOSIS.—Clearly a member of the genus *Chlorostilbon* because of the entirely steel-blue, forked tail of the males, and the distinct dusky face and cheeks and white postocular stripe and uniform gray underparts of the females. Size significantly larger than any other South American form of *Chlorostilbon* (exposed culmen always >18 mm, vs 17 mm or less in all other forms); total culmen >21 mm vs <19.5 mm; wing chord >48 mm in males, >47 mm in females, vs <47.5 mm and <46.5 mm respectively, except for the isolated *C. mellisugus duidae,* which may reach 49.5 mm in both sexes; and weight usually >3.5 g, vs <3 g). Differs from all forms of *C. mellisugus* in having the basal half of the mandible red in males, or with a trace of red in females; in the dull, non-iridescent crown (males) and extensively grey bases of the lateral rectrices (females). In these characters resembles *C. gibsoni* from north and west of the Andes, but differs from all forms of *gibsoni* in having the tail much more shallowly forked, with the lateral rectrices more truncate (males) to rounded (females) at the tip, and the breast and throat much more strongly bluish in color (males). In the latter feature is most like *C. aureoventris* of southeastern South America, but always lacks red on the upper mandible (which is extensively red in the latter); females of *aureoventris* also lack gray on the lateral rectrices.

ETYMOLOGY.—I take pleasure in naming this species for Fr. Antonio Olivares in honor of his many pioneering contributions to Colombian ornithology and his indefatigable labor in building the bird collection of the Instituto de Ciencias Naturales. The English name refers to the isolated mountain range which includes the type locality and evidently encompasses the entire distribution of the species.

DESCRIPTION OF HOLOTYPE.—(Color nomenclature follows Smithe 1975, 1981). Crown, nape, back, and rump metallic green, near 162, Shamrock Green; a few feathers of the nasal area of the anterior forehead more brilliant golden green (near 158, Chartreuse); a small grayish-white postocular spot. Upper tail-coverts more bluish green (163, Emerald green); tail dark steely blue, nearest 90, Blue-black. Facial area and sides of neck brilliant Emerald Green, with Chartreuse reflections, passing abruptly to brilliant blue-green (between 164, Cyan, and 65, Turquoise Blue, depending on viewing angle) over the entire throat and upper breast, this passing to brilliant green (near 62, Spectrum Green) on the lower breast and belly; lower tail coverts more bluish, near Emerald Green; a small tuft of downy white feathers on the thigh. Remiges blackish with faint bluish gloss (near 73, Indigo). Basal 3/4 or more of lower mandible red (between 13, Geranium Pink, and 10, Ruby); rest of bill, legs, and feet black. Exposed culmen 19.5 mm, total culmen 21.8 mm, wing chord 49.6 mm, tail length 25.6 mm, tarsus 4.4 mm, weight 3.4 g. Adult male, left testis 2.4 × 2.3 mm, no fat; tiny diptera in stomach.

DESCRIPTION OF ADULT FEMALE (based on ICN 31244).—Upperparts somewhat more bronzy-green than in the adult male, nearer 60 (Parrot Green), somewhat duller on the crown; the more worn feathers of the back with more bluish tips (near Emerald Green), producing a slightly scaly effect; longest upper tail coverts and most of central rectrices more bluish (between Emerald Green and Cyan but darker); the second and third pairs of rectrices similar, but shading to dark blue (near 173, Indigo Blue) at the tips. The outer two rectrices are extensively pale gray basally (near 86, Light Neutral Gray), with the medial portion Indigo Blue; the outermost rectrix is tipped broadly, the fourth and third progressively more narrowly, with Light Neutral Gray. The malar and auricular areas are dark sooty gray, tinged with dull bronze; a white stripe extends from the eye back over the auriculars. The underparts are pale gray, slightly tinged brownish (near 79, Glaucous, but paler), averaging palest on the throat and darkest on the upper breast. The basal 1/4 of the lower mandible is tinged with dark red, the rest of the bill and feet are black.

PLUMAGE VARIATION IN THE TYPE SERIES.—Variation among the adults of the type series is slight in both sexes, reflecting chiefly feather wear (the degree of 'scaliness' in the dorsal plumage, the degree to which the crown is dull and soiled in females); one female (ICN 31245) has the tip of the first rectrix tinged with blue. The subadult male (ICN 31253) is approaching adult plumage, with the brilliant feathers below colored as in the adults but more scattered over a dull, dusky green juvenal plumage; traces of a dusky mask and whitish postocular and malar stripes remain; the tail is less forked than in the adult males, and the outer rectrix is very narrowly tipped with dull gray. The subadult female (ICN 31243) is a more uniform, bronzy green dorsally with no bluish tinge to the upper tail coverts or central rectrices, and a darker, duller gray below.

ADDITIONAL SPECIMENS EXAMINED.—Between May and August 1993, Diego Silva and Tomas Walschburger of the Fundación Puerto Rastrojo, conducted studies of birds in the area of the Río Mesay, just south of the border of the National Park (0°4′N, 72°26′W), some 85 km SSE of our study area. They observed and collected birds along a transect from the river (ca 230 m elevation) to the top of a low mesa (ca 360 m), an isolated southern outlier of the main Sierra. Four specimens of *C. olivaresi* were taken in the scrub atop the mesa in July 1993 and were available for examination. These specimens agree perfectly in measurements and coloration with the type series, allowing for differences in plumage wear: in particular, the golden-green reflections of the facial area and sides of the neck of the males are stronger, increasing the contrast with the bluish green of the throat. The adult male specimen from the 1990 expedition does not differ from the males of the type series. Thus, the characters of *C. olivaresi* appear to be uniform over most or all of the Sierra de Chiribiquete.

THE SIERRA DE CHIRIBIQUETE AND THE ECOLOGY OF *C. OLIVARESI*

The Sierra de Chiribiquete consists of a series of sandstone mesas and buttes some 125 km long and 30 km wide, extending in an arc that curves from NW–SE in the north to NE–SW in the south, between the latitudes of 1°20′N and 0°20′N, centered along the line of 73°W longitude (Fig. 1). The mesas rise abruptly from the surrounding flat lowlands to heights of 800–900 m in the north and 600 m in the south, often presenting several levels or terraces separated by vertical cliffs. Many of the larger mesas are riven by spectacular chasms or cracks; the flat upper surfaces are drained by streams flowing through vertical cracks that emerge as waterfalls at the edges of the mesas. The thin, sandy soil of the table-tops supports a scrubby vegetation interspersed with areas of naked rock: the stature of the vegetation reflects the depth of the soil (or the absence thereof) at any given point. Further details of the topography, vegetation, and geology of the Sierra de Chiribiquete are given by Estrada and Fuertes (1993). Extending south of the main part of the Sierra are a series of progressively lower mesas (ca 300–350 m) which reach the Río Caquetá at Araracuara (ca 0°30′S).

The base camp of our expedition was situated on the flat middle level of a large (ca 3 km long) mesa at an elevation of 570 m. To the north and east, a line of cliffs rises abruptly to the top level of the mesa (ca 700 m); to the west, the mesa is bounded by a steep-sided canyon some

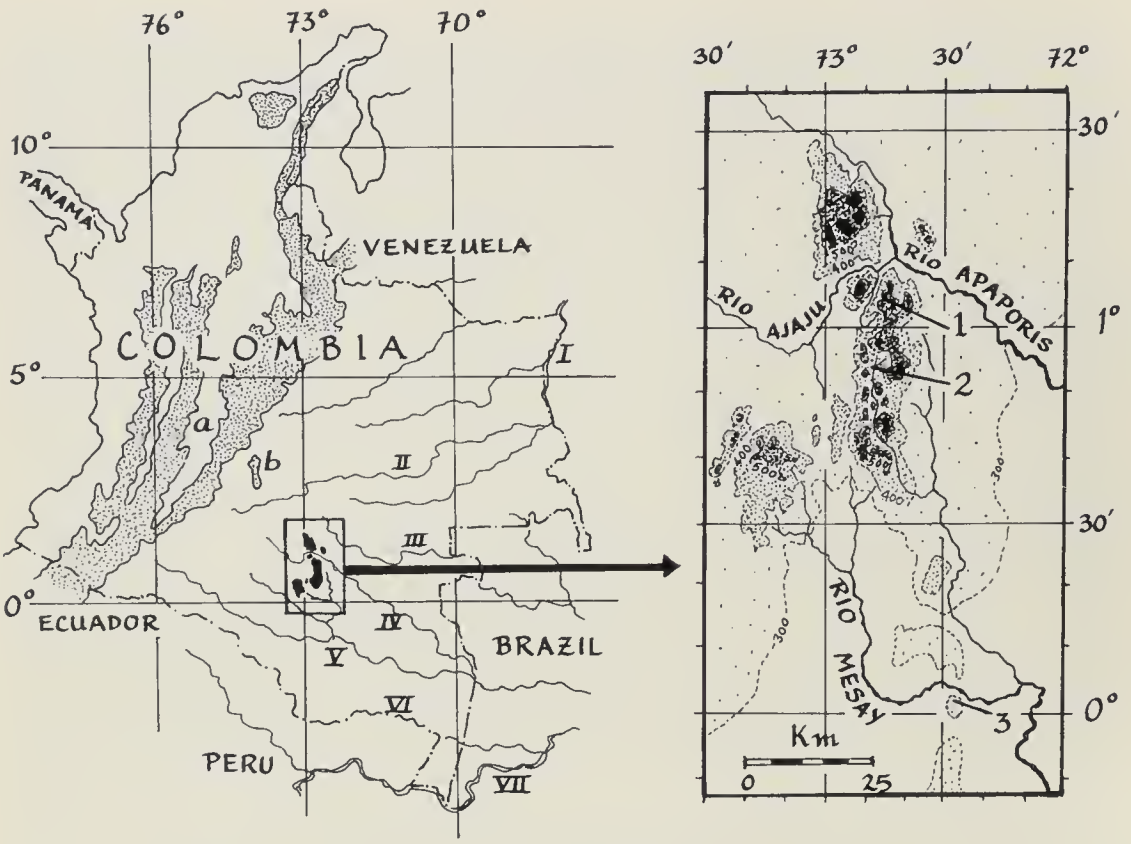

FIG. 1. *Left:* location of the Sierra de Chiribiquete (inset) in relation to the major mountain ranges (stippled) of Colombia, and the major rivers of SE Colombia and adjacent areas (Roman numerals). The rivers are I. Orinoco; II. Guaviare; III. Vaupés; IV. Apaporis; V. Caquetá; VI. Putumayo; and VII. Amazon. Other localities indicated are a. Magdalena Valley and b. Sierra de la Macarena. *Right:* The Sierra de Chiribiquete and adjacent areas showing major rivers and the collecting localities for *Chlorostilbon olivaresi*. The 300, 400, 500, and 600 m contour lines are indicated. Localities: 1. Type locality (Valle de los Menhires); 2. Collecting site of December 1990 specimen (Valle de las Abejas); 3. Río Mesay site. Redrawn from Estrada and Fuertes 1993, in part.

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FIG. 2. Landforms and vegetation at the type locality. A. General topography, showing the butte and our campsite, with adjacent stunted forest and surrounding *Bonnetia* scrub of the middle level of the mesa; taller forest at the base of the fringing cliffs in foreground and other mesas just visible in the background. B. Aspect of *Bonnetia* scrub, the most important habitat of *C. olivaresi*. Note areas of naked rock and patches of low vegetation (mainly *Navia garcia-barrigae*) in foreground, the stiff, coriaceous-succulent leaves of many shrubs (*Graffenriedia* sp. in foreground, *Clusia chiribiquetensis* at center. The low shrub L of center is *Decagonocarpus cornutus*, the most important nectar source of *C. olivaresi*; taller shrubbery in background (with large white flowers) is *Bonnetia martiana*.

100–150 m deep that slopes steeply down towards the surrounding lowlands. The base camp was located some 100 m SE of the base of an isolated butte that rises precipitously to a height of ca 75 m.

The vegetation around the base camp consisted of open scrub dominated by the shrub *Bonnetia martiana* (Theaceae); patches of dense scrub, in which the taller shrubs attained a height of 2–3 m, alternated with patches of low, savannalike vegetation and areas of naked rock (Fig. 2). The principal shrubs of the area had thick, coriaceous leaves and twigs suggesting adaptation to resist drought, doubtless reflecting the shallow, sandy soil with low nutrients and minimal water retention capacity. The most common shrub species included, besides *Bonnetia, Clusia chiribiquetensis* (Guttiferae), *Tepuianthus savannensis* (Tepuianthaceae), *Graffenriedia* sp. (Melastomataceae), and *Decagonocarpus cornutus* (Rutaceae). Between the shrubs, and in slight depressions where a thin layer of sandy soil accumulated, occurred a low herbaceous vegetation dominated by Xyridaceae, Eriocaulaceae, Burmanniaceae, Cyperaceae, and *Vellozia phantasmagorica* (Velloziaceae) with only occasional grasses (Gramineae); where drainage was impeded, pools formed after every rain in which *Utricularia* spp. (Lentibulariaceae) were abundant. Areas of bare rock were colonized by a terrestrial bromeliad, *Navia garcia-barrigae.* A low, dense, tangled forest (canopy height 3–5 m) dominated by *Clusia* spp. and *Licania* sp. grew around the base of the butte.

The level of the mesa sloped very gently towards the fringing cliffs to the north and east, at the bases of which grew a much taller forest (canopy height 20–25 m) with numerous palms and a relatively well-developed understory; in the canyon bottom grew a forest of similar canopy height but with few palms and notably low tree species diversity and a few large-leaved monocots (*Heliconia, Calathea, Costus, Phenakospermum*) in the understory. The northern part of the mesa was drained by a stream along which grew an extremely dense, tall (canopy ca 5 m) stand of *Bonnetia* whose tangled aspect suggested that of a young mangrove swamp. A general inventory of the avifauna and its biogeographical affinities (Stiles et al. 1995), and a detailed analysis of mist-net captures in relation to vegetation characteristics (Díaz et al. 1996) will appear elsewhere.

In the study area, *Chlorostilbon olivaresi* was fairly common in the open *Bonnetia* scrub of the mesa, where 12 of the 15 individuals were captured; in fact, it was the bird most frequently captured in mist-nets in the open areas of the mesa. In this habitat, both sexes were observed visiting only the red-orange flowers of *Decagonocarpus cornutus* (see Frontispiece) and were frequently noted gleaning small arthropods from the foliage and flowers of *Bonnetia* and other shrubs and flycatching at breaks in the vegetation, especially in late afternoon. Pollen samples taken

from the beaks of eight mist-netted birds with transparent Scotch tape contained only pollen of *Decagonocarpus*, usually <10 grains (5 cases), three grains of pollen of *Decagonocarpus* and one of *Bonnetia* (one bird), or no pollen at all (2 birds). The visit to *Bonnetia* was almost certainly to obtain insects such as thrips which were often present on the large, open, and fragrant camellialike flowers of this species (which do not produce nectar). Stomach contents of collected individuals contained tiny insects, mainly flies, but a few thrips and/or microhymenopterans were present in at least two stomachs. The only other hummingbirds to occur regularly in the *Bonnetia* scrub were the Versicolored Emerald (*Amazilia versicolor*), which also visited *Decagonocarpus* but was much scarcer; and the Black-throated Mango (*Anthracothorax nigricollis*), which appeared to be more insectivorous and was seen to visit only the flowers of a small tree of the Bombacaceae in the low forest at the base of the butte. We never saw any interactions between any of these species.

The only other habitat in which we regularly recorded *C. olivaresi* was the forest at the base of the fringing cliffs at the north end of the mesa. Here, small numbers occurred in the understory and at gaps; three birds were captured, and on several occasions a female was observed visiting the flowers of a small understory tree of the Violaceae. In several days of observation and netting, we never encountered *C. olivaresi* in the forest of the canyon bottom. In visits to other areas at the base of the Sierra, including mist-netting, other members of the expedition (A. Repizzo, B. Ortiz) never encountered *C. olivaresi* in the forests at lower elevations. During their work at the Río Mesay site, Silva and Walschburger only recorded *C. olivaresi* in the *Bonnetia* scrub on the top of the mesa or in the adjacent low forest (340–360 m), never lower or closer to the river. The 4–6 months difference between the dates of our observations and those of Silva and Walschburger would appear to preclude the possibility of extensive seasonal movements (e.g., into the surrounding lowland forests) by this hummingbird. Thus, *C. olivaresi* may be restricted to the scrubby vegetation and adjacent forests on the mesas of the Sierra, and it is quite probably absent from the surrounding forested lowlands. It evidently occurs widely in the Sierra de Chiribiquete, given the distance between the Río Mesay site and the type locality; the 1990 specimen was taken some 20 km south of the type locality, also in *Bonnetia* scrub at a slightly lower elevation (ca 420 m). The southern limit of *olivaresi* remains to be determined but is evidently somewhere between the Río Mesay and the Río Caquetá, since it was not taken during intensive collecting by H. Romero at Araracuara in similar *Bonnetia* scrub.

Of the specimens of *C. olivaresi* we collected, one adult male and two females (as well as both of the subadults) had the gonads small and

undeveloped; one male and one female had moderately enlarged gonads. Among the birds measured and released, one female had a developing brood patch. The two subadult specimens were at least several months old, as they had lost their bill corrugations. Taken together, these data indicate that *C. olivaresi* was at the start of its breeding season during our observations, although courtship displays were not observed, and we found no active nests. None of the individuals captured were molting, and most were in slightly to moderately worn plumage, consistent with the inference that the breeding season was beginning (cf Stiles 1985b). Although meteorological data for the Sierra de Chiribiquete do not exist, extrapolation from the data for other sites in Colombian Amazonia suggest that our expedition took place at the very beginning of the dry season (Estrada and Fuertes 1993). Flowering of at least *Decagonocarpus,* evidently the most important nectar source at this time for *C. olivaresi,* was definitely increasing during our observations (many flower buds, few developing fruits). Fruiting of several species was also increasing or about to begin in late November 1992, and a number of other bird species were evidently just starting gonadal maturation, suggesting that the dry season might include the main breeding period for a considerable segment of the Chiribiquete avifauna (Stiles et al. 1995).

The four Río Mesay specimens, taken in July 1993, were for the most part in very fresh plumage, and one female was in heavy molt; neither of the two with gonad data were in breeding condition. If the seasonality of the two sites is similar, this suggests that the breeding season of *C. olivaresi* falls between late November or December and perhaps May. Molt in the population extends from perhaps May through at least July, as both males and one female of the Río Mesay specimens had completed molt by July; in hummingbirds it is not unusual for males to molt a month or so ahead of females (cf Stiles 1985b).

Like other members of its genus, *C. olivaresi* is a rather quiet hummingbird under most circumstances. The only vocalization heard was a sharp, dry, scratchy "cht", similar to the calls of other *Chlorostilbon* but somewhat louder, and given by birds foraging at flowers. We never heard it sing. Compared to others of the genus I have observed, *C. olivaresi* is less nervous and flighty at flowers and shows much less of the incessant rapid flicking or pumping of the tail while foraging (cf Stiles and Skutch 1989).

PATTERNS OF VARIATION IN THE *C. MELLISUGUS* COMPLEX IN NORTHWESTERN SOUTH AMERICA

No fewer than 10 forms in this complex are recognized by most authors from Colombia and adjacent areas of northwestern South America (see Table 1, Fig. 3). Because *C. olivaresi* appears to be a member of this

TABLE 1

CURRENTLY ACCEPTED SUBSPECIES OF THE *CHLOROSTILBON MELLISUGUS* COMPLEX IN NORTHWESTERN SOUTH AMERICA, WITH THEIR DISTRIBUTIONS AND DIAGNOSTIC CHARACTERS[a]

Subspecies	Distribution	Characters[f]
pumilus	W Colombia from Pacific slope of W Andes E to W edge of Magdalena Valley	Bill black. M: tail moderately forked; glittering crown; breast with little or no blue. F: trace of grey in outer rectrices, extensive green in central rectrices.
melanorhynchus[b]	Extreme SW Colombia (Nariño) and W Ecuador	Like *pumilus* but averaging larger.
gibsoni	Upper and middle Magdalena Valley Colombia	Lower mandible largely red. M: tail very deeply forked, outer rectrices attenuate; breast green; crown dull. F: outer rectrices with extensive grey bases, broad whitish tips.
chrysogaster	N lowlands of Colombia E to Santa Marta; W of Lago de Maracaibo, Venezuela–Colombia	Like *gibsoni* but M: tail even more deeply forked, forecrown glittering, throat and breast tinged blue; F: grey of outer rectrices darker, less extensive.
nitens[c]	Arid N coast of extreme NE Colombia and NW Venezuela	Like *chrysogaster* but tail of M slightly less deeply forked.
caribaeus[d]	Most N coastal region of Venezuela, S to Orinoco region and Llanos of Colombia	Bill black. M: glittering crown; breast with trace of blue; tail shallowly forked. F: at most a trace of dusky on lateral rectrices, otherwise blue.
napensis[e]	SE Colombia S of Llanos; E Ecuador; adjacent NE Perú	Like *caribaeus* but averaging larger. M: tail very shallowly forked, nearly truncate, breast strongly tinged blue. F: extensive green flecking on sides.
phaeopygos	E Perú to NE Bolivia, incl. adjacent Brazil	Like *napensis* but M: belly duller, darker, less contrast with blue of breast; F: much less green flecking below. Also averages larger, especially tail.
subfurcatus	S+SE Venezuela E to Guayana, and adjacent NW Brazil	Like *caribeus* but M: tail less forked, breast more bluish. Averages slightly larger.
duidae	Mt. Duida, SE Venezuela	Like *subfuratus* but decidedly larger; M: tail longer, more forked; breast less bluish.

[a] Characters and distributions from Meyer de Schauensee (1964, 1966); Meyer de Schauensee and Phelps (1978); Zimmer (1950), and Zimmer and Phelps (1952).
[b] May not be distinct from *pumilus*.
[c] May not be distinct from *chrysogaster*.
[d] Includes *nanus* from the Orinoco region.
[e] Often lumped with *phaeopygos*.
[f] M = male, F = female.

complex, I decided that to evaluate properly its status and affinities a broader analysis of the patterns of variation in the complex over northwestern South America would be required.

Previous studies.—The first comprehensive study of the *mellisugus* complex was that of Zimmer (1950) who concluded that the mosaic nature of the patterns of geographic variation, plus the allopatric distributions of most forms, justified considering all forms of the complex as subspecies of a single, variable species *mellisugus.* However, several points of confusion exist in his analysis. Evidently, Zimmer started by considering two forms from northern South America, *nitens* and *chrysogaster,* as members of different subspecies groups and later concluded that they might not be separable at all, thus favoring lumping the "eastern" and "western" groups.

In his initial study of the birds of Colombia, Meyer de Schauensee (1948–1952) had considered all Colombian forms of the complex as subspecies of *gibsoni,* but he later (1960, 1966) noted that two groups of races could be distinguished on the basis of bill color: those with the lower mandible largely red (*gibsoni, chrysogaster,* and *nitens*) and those with all-black bills (all other forms). He noted that the red-billed forms were also those with the most deeply forked tails and attenuated outer rectrices in the males, and with the most gray in the rectrices of the females. He noted apparent sympatry of a red-billed (*gibsoni*) and black-billed (*pumilus*) form without evident intergradation at two localities on the western edge of the Magdalena Valley in Colombia and concluded that two species should be recognized in Colombia: the red-billed *gibsoni* (including *chrysogaster* and *nitens*) and the black-billed *mellisugus* (including *pumilus, melanorhynchus, caribaeus,* and *phaeopygus* (=*napensis*).

Wetmore (1968) adopted Meyer de Schauensee's character of bill color as a criterion for distinguishing species in the complex when he separated the black-billed *assimilis* of southwestern Costa Rica and W Panamá from the red-billed *canivetii* of farther north. The arrangement of Meyer de Schauensee (1960, 1966) has been followed by recent authors for the South American forms of the complex (Meyer de Schauensee and Phelps

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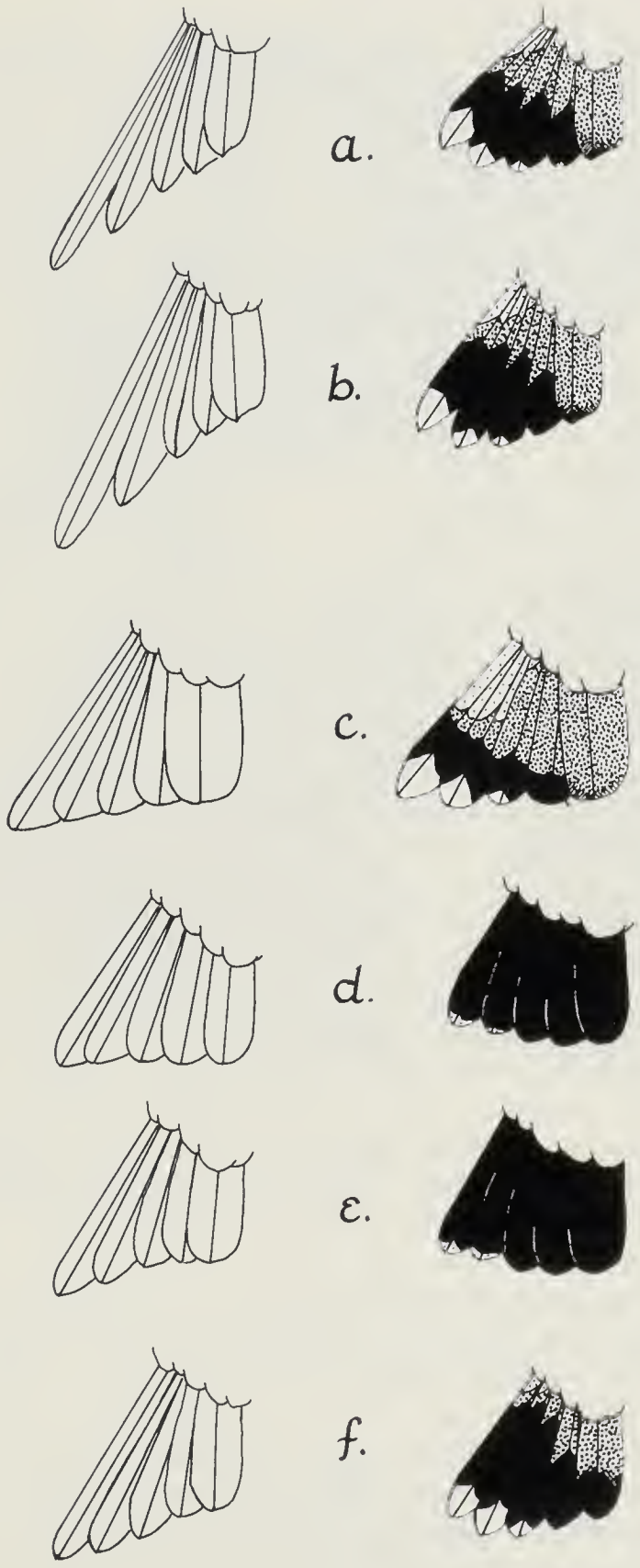
FIG. 3. Tails of members of the *C. mellisugus* complex from Colombia, drawn to the same scale. Left: tails of adult males, showing form of rectrices; in all, rectrices are uniform steely blue-black. Right: tails of adult females, showing form, pattern, and colors of the rectrices. Solid: steely blue-black; heavy stipple: green; light stipple: grey; open: white. The forms illustrated are: a. *chrysogaster*; b. *gibsoni*; c. *olivaresi*; d. *napensis*; e. *caribaeus*; f. *pumilus.*


a.
b.
c.
d.
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f.

1978, Hilty and Brown 1986, Sibley and Monroe 1990). However, because the characters of *olivaresi,* as detailed above, appear to be in part a mosaic of features of *gibsoni* and *mellisugus* as currently recognized, this arrangement requires a detailed reevaluation. For this analysis, I consulted specimens of the *mellisugus* complex available in the following museums (numbers of specimens in parentheses): the Instituto de Ciencias Naturales, Universidad Nacional de Colombia (69); the Universidad de La Salle, Bogotá (12); the Unidad de Investigación "Federico Medem" (UNIFEM), INDERENA (6), Bogota; and the Colegio de San José, Medellín (8). For each specimen, I measured the exposed culmen, total culmen, wing chord, and tail length to the nearest 0.1 mm with dial calipers. For males only, I measured the depth of the tail fork as the difference between the lengths of the first and fifth rectrices. In addition, I took detailed notes on color characters of each form and made detailed drawings of the rectrices of representative individuals of both sexes of all forms (Fig. 4). Field work in various parts of Colombia has also given me the opportunity to capture and measure an additional 18 individuals of various forms of the *mellisugus* complex. For these birds, I made the preceding measurements except depth of tail fork, also with dial calipers, and to the same level of accuracy; I also weighed all birds to the nearest 0.1 g with a 10 g Pesola spring balance. Because in previous studies I had found that my field measurements did not differ from those taken in the museum and that my measurements of birds in the field agree closely with remeasurements of the same birds prepared as museum specimens (Stiles 1985a, 1995), I have included both types of measurements in the quantitative analyses below. In addition, M. Marín kindly measured 10 specimens of *uapensis* and *pheaopygus* in the collection of the Museum of Natural Science, Louisiana State Univ. Having worked with and measured birds previously with Marín, I am confident that his measurements are comparable with mine and have incorporated them into the analyses.

In all, measurements from 111 specimens of the following forms were used in the analyses: *olivaresi, pumilus, gibsoni, chrysogaster, caribaeus,* and *uapensis* (Table 2). Of the remaining forms in Table 1, none occurs in areas adjacent to *olivaresi* and is likely to bear upon its status; I was able to examine only two specimens of *nitens,* and none of *melanorhynchus, subfurcatus, duidae,* or *phaeopygus.* For the characters of these forms (Table 1), I have relied upon the descriptions of Zimmer (1950) and Zimmer and Phelps (1952). For the six forms mentioned above, measurements were analyzed by one-way analysis of variance (ANOVA) for each sex separately. Where a significant result was obtained in the ANOVA, Tukey a posteriori tests were performed to determine which forms differed significantly with respect to the measurement in question (Zar

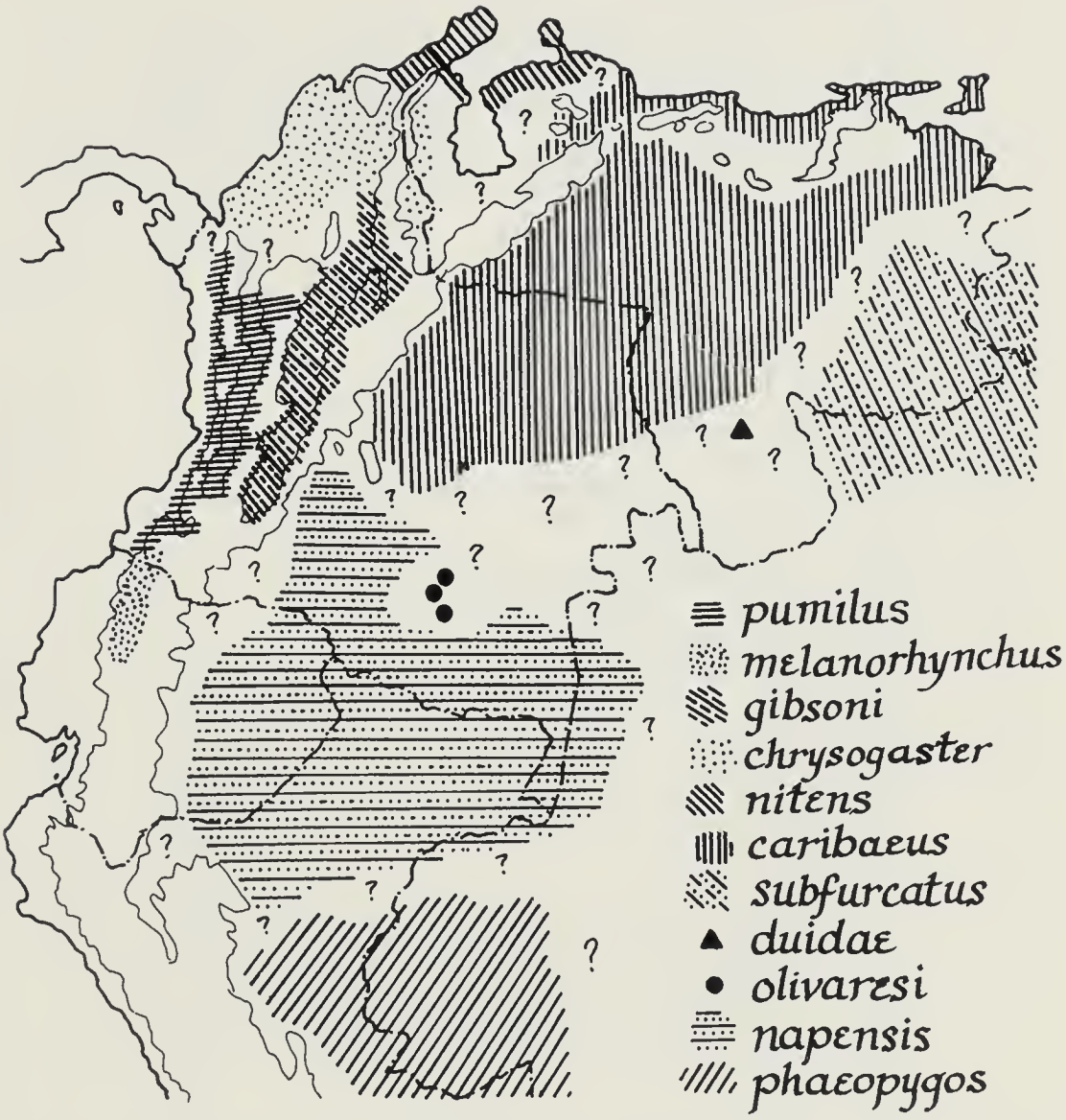

FIG. 4. Distributions of the members of the *C. mellisugus* complex in northwestern South America. Note that limits of some forms are imperfectly known, as are possible zones of contact; especially east of the Andes, distributions are probably more continuous than shown, but collecting localities are often widely scattered.

1988). For the measurement of depth of tail fork, I derived a measure of "relative tail fork" by dividing the difference r5-r1 by the tail length for each specimen, to control for differences in absolute size between the various forms.

The most striking result of the analyses of variance of the measurements (Table 3) is the clear-cut separation of *olivaresi* (at a significance level of $P < 0.001$) from all other forms of the *Chlorostilbon mellisugus* complex, with respect to bill length (both exposed and total culmen), wing

TABLE 2

MEASUREMENTS[a] OF VARIOUS FORMS OF THE *CHLOROSTILBON MELLISUGUS* COMPLEX FROM COLOMBIA AND ADJACENT AREAS

Form	Sex	N	Exposed culmen	Total culmen	Wing chord	Tail length	Relative tail fork	Body mass (N)
pumilus	M	12	14.09 ± 0.63	16.09 ± 0.92	46.02 ± 1.01	24.71 ± 1.02	0.252 ± 0.039	2.63 ± 0.18 (4)
	F	10	14.73 ± 0.78	16.41 ± 0.88	44.91 ± 0.91	23.64 ± 1.12		2.57 ± 0.21 (6)
gibsoni	M	12	15.38 ± 0.53	17.98 ± 0.66	46.48 ± 0.76	26.30 ± 1.06	0.411 ± 0.041	2.79 ± 0.17 (4)
	F	9	15.80 ± 0.51	18.36 ± 0.68	45.14 ± 0.71	23.88 ± 1.25		2.65 ± 0.20 (4)
chrysogaster	M	9	15.10 ± 0.42	17.38 ± 0.59	42.90 ± 1.09	27.43 ± 1.43	0.462 ± 0.046	
(N. coast)	F	4	15.90 ± 0.56	18.55 ± 0.66	43.05 ± 0.69	23.88 ± 1.05		
chrysogaster	M	5	15.23 ± 0.25	17.65 ± 0.54	45.86 ± 0.36	27.70 ± 0.67	0.419 ± 0.021	
(Nrt. Sant.)	F	5	16.38 ± 0.41	18.58 ± 0.31	44.88 ± 0.92	25.62 ± 0.60		
caribaeus	M	10	14.80 ± 0.59	16.93 ± 0.91	43.69 ± 1.03	21.25 ± 0.89	0.203 ± 0.20	2.68 ± 0.18 (6)
	F	6	15.47 ± 0.72	18.08 ± 0.91	42.58 ± 1.14	21.47 ± 0.93		2.54 ± 0.23 (4)
napensis	M	8	15.89 ± 0.59	17.91 ± 0.83	44.81 ± 1.34	21.36 ± 1.08	0.094 ± 0.031	2.73 ± 0.25 (4)
	F	6	15.90 ± 0.64	17.73 ± 1.28	42.47 ± 0.48	21.05 ± 0.70		2.37 ± 0.32 (3)
olivaresi	M	7	20.29 ± 0.45	22.44 ± 0.68	49.77 ± 0.63	25.71 ± 0.59	0.184 ± 0.019	3.78 ± 0.26 (6)
	F	12	20.91 ± 0.85	22.91 ± 0.61	48.60 ± 0.60	24.63 ± 0.87		3.60 ± 0.22 (11)

[a] Mean and standard deviation. Masses are in g; culmen, wing chord, and tail length are in mm.

TABLE 3

RESULT OF ANALYSES OF VARIANCE COMPARING MEASUREMENTS OF MEMBERS OF *CHLOROSTILBON MELLISUGUS* COMPLEX FROM NORTHWESTERN SOUTH AMERICA

Measurement	Sex	*F*	*P*	Result of Tukey tests[a]
Exposed culmen	M	109.19	<0.001	PU CA CC CN GI NA OL
	F	94.75	<0.001	PU CA GI NA CC CN OL
Total culmen	M	53.90	<0.001	PU CA CC CN NA GI OL
	F	71.83	<0.001	PU NA CA GI CC CN OL
Wing chord	M	48.81	<0.001	CC CA NA CN PU GI OL
	F	65.53	<0.001	NA CA CC CN PU GI OL
Tail length	M	53.08	<0.001	CA NA PU OL GI CC CN
	F	17.57	<0.005	NA CA PU GI CC OL CN
Body mass	M	29.64	<0.001	PU CA NA GI OL
	F	42.47	<0.001	NA CA PU GI OL
Relative tail fork	M	103.89	<0.001	NA OL CA PU GI CN CC

[a] Abbreviations: CA = *caribaeus*; CC = *chrysogaster*—N coast of Colombia; CN = *chrysogaster*—Norte de Santander, NA = *napensis*; GI = *gibsoni*; OL = *olivaresi*; PU = *pumilus*.

Forms not significantly different ($P < .05$) in a given measurement are connected by solid lines. Breaks in the lines indicate significant differences, and the number of slashes indicates the degree of significance: one slash = $P < 0.05$; two slashes = $P < 0.01$; three slashes = $P < 0.001$.

chord, and mass. The larger size of *olivaresi* is most dramatically shown by the data on body mass, perhaps the best indicator of overall size: this form is fully 35–40% heavier than all the other forms, which do not differ among themselves. In fact, *olivaresi* is apparently the largest form in the

entire genus *Chlorostilbon,* exceeding in size even the Cuban Emerald *C. ricordii* (cf Ridgway 1911, Howell 1993). Regarding measurements of the tail, the separation of *olivaresi* is more equivocal, chiefly because this form, because of its overall large size, has a tail length more similar to those of the *gibsoni* group with their relatively long, deeply forked tails, but in its shallowly forked tail, *olivaresi* resembles closely various members of the *mellisugus* group.

Although some of the remaining forms differed significantly from others in one or another dimension, similar clean-cut separations between groups were the exception. Males of the *gibsoni* group differed from those of the *mellisugus* group significantly in tail length and highly significantly in relative depth of tail fork; however, in most other dimensions the pattern was less clear: often differences significant in one sex were not so in the other, and the rank order of the forms often varied from one measurement to another and/or between the sexes for a given measurement (Tables 2, 3). This is undoubtedly at least in part a reflection of the mostly small sample sizes (Table 2). One interesting result was the significant difference in wing length between the northern and cis-Andean populations of *chrysogaster*; however, these populations were similar in other dimensions. Aside from *olivaresi,* the most distinctive form, in terms of measurements, was *pumilus,* with its unique combination of a very short bill and a relatively long wing (Table 3; see below).

Patterns of plumage variation.—In eastern Colombia, specimens of *caribaeus* showed no obvious variation between Arauca and Meta (in particular, those from Arauca showed no tendency to approach *chrysogaster*). To the south, *napensis* differed in having a shorter, less forked tail and more strongly bluish throat in the males, more lateral green flecking below and less pale tipping on the outer rectrices in the females, and a somewhat longer bill in both sexes. I could detect no consistent differences in size or color between specimens of *napensis* from extreme southern Meta, northwestern Caquetá, eastern Vaupés, or southern and eastern Amazonas in Colombia, or (in size at least) eastern Ecuador or extreme northeastern Peru. The largest male measured was from eastern Peru, where the range of this form approaches that of the possibly indistinguishable *phaeopygos.* I have not seen specimens of *phaeopygos* from Peru, so cannot comment on the validity of separating *napensis*; however, female specimens of the latter I have seen do show the extensive green flecking below used by Zimmer (1950) to distinguish this race from *phaeopygos* and *caribaeus.* Although *napensis* and *caribaeus* differed significantly in relative tail fork in this analysis (Table 3), it is worth noting that this difference is apparently bridged by the adjacent *subfurcatus* and *duidae,* to judge from the measurements of these forms given by Zimmer

and Phelps (1952). I should note in passing that my measurements are in reasonably close agreement with those of Zimmer for those forms which we both measured.

The range of *olivaresi* appears to be nearly completely nested within that of *napensis*. Although I have seen no specimens of the latter from localities adjacent to the Sierra de Chiribiquete, those from northwest, south, and east of this range show no approach to the characters of *olivaresi*; in fact, *napensis* differs from *olivaresi* in most characters at least as much as does any other cis-Andean form of the *mellisugus* complex. This indicates that gene flow between *olivaresi* and *napensis* does not occur; given the great difference in size, it is highly questionable whether interbreeding could occur at all.

Within the *gibsoni* group, *chrysogaster* males have a glittering forecrown and usually, at least, a faint bluish tinge to the throat (more than either *pumilus* or *gibsoni*). The tail is even more deeply forked than in *gibsoni*; in females, the pattern of the tail is similar, although the gray area at the bases of the outer rectrices tends to be darker and less extensive. The difference in wing length between the populations of this form east and west of the Serranía de Perijá is interesting: at the very least, it appears that the former shows no approach to the geographically adjacent form of *mellisugus, caribaeus*. In color, pattern, and tail shape, the cis-Andean population of *chrysogaster* also appears as different from *caribaeus* as does the trans-Andean population, suggesting that gene flow between these populations is not occurring. The little information I have on *nitens* suggests that this form is very similar to the trans-Andean *chrysogaster*. Although data are required on possible zones of contact between *nitens* and *caribaeus,* the information currently available again favors maintaining separate species status for the *gibsoni* group (including *chrysogaster* and *nitens*) and *mellisugus*.

The case of C. pumilus.—This form of western Colombia agrees with members of the *mellisugus* group in having an all-black bill, in the glittering crown of the males, and in the virtual absence of grey in the outer rectrices of the females. However, the males have significantly longer, more deeply forked tails and less bluish breasts than do any of the eastern forms of this group. Females of *pumilus* differ from those of the eastern races in their slightly forked to double-rounded tails, with extensive green in most rectrices, and in the more extensive pale tips to the outer rectrices, as well as in showing some dark gray at the bases of these rectrices. In overall proportions, *pumilus* has a shorter bill and longer wing and tail than do the eastern races, sex for sex.

In several of these characters, *pumilus* rather resembles the adjacent *gibsoni* of the Magdalena Valley; however, it differs strongly from *gibsoni*

in bill color, tail shape, bill length, crown color (males), and the color of the outer rectrices (females). Moreover, these differences appear to be as great in specimens from areas where the two forms approach each other (western Tolima, western Antioquia), as in areas far from the possible contact areas. Hence, the evidence presently available favors continuing to separate *pumilus* and *gibsoni* at the species level.

Considering the next form to the north, *assimilis, pumilus* also shows a number of clear-cut differences based upon the measurements, weights, and descriptions of the latter in Wetmore (1968). In males, the crown of *pumilus* is highly iridescent, while in *assimilis* it is plain; the gray of the outer rectrices of the females is much more extensive in *pumilus*. In measurements, *pumilus* has a much shorter bill, longer wing, and shorter tail and also weighs considerably less in both sexes. The ranges of the two forms are separated by a wide gap in eastern Panamá (cf Wetmore 1968) but from my observations of both forms in the field, I suspect that they differ in ecology, with *pumilus* preferring significantly wetter areas than does *assimilis*. I conclude from this analysis that *pumilus* is best considered an allospecies in the *mellisugus* superspecies rather than as a subspecies of *mellisugus* (sensu stricto); this also eliminates the disjunct distribution of the latter (with *pumilus* separated by *gibsoni* from the other forms of *mellisugus*).

Although I was unable to examine specimens of *melanorhynchus,* there seems little reason to doubt that this form is conspecific with *pumilus*; Zimmer (1950) noted that the two differ little, if at all, in coloration and overlap in measurements and, in fact, might not be separable. The two forms were supposed to differ in their preferred elevations, with *melanorhynchus* occurring mostly above 2000 m, and *pumilus* at lower elevations; however, this difference also tended to break down in the series of specimens available to Zimmer (1950). If *pumilus* and *melanorhynchus* are considered to comprise a separate allospecies in the *mellisugus* complex, as I feel the evidence indicates, this species will have to be called *C. melanorhynchus* (since *melanorhynchus* Gould 1860 has priority over *pumilus* Gould 1872). Without having seen specimens of *melanorhynchus* itself, I cannot comment on the advisability of synonymizing *pumilus* and recommend further study.

On the basis of a phylogenetic species concept (Cracraft 1983, McKitrick and Zink 1988), *melanorhynchus* (with *pumilus*) would also clearly be entitled to species status; it possibly differentiated from other forms of the *mellisugus* complex in the Chocó humid forest refugium during one of the dry epochs of the Pleistocene (cf Haffer 1974). I suggest the English name West Andean Emerald for this form in view of its basically

Andean distribution, which lies to the west of all other members of the *mellisugus* complex in South America.

Origin of the Chiribiquete Emerald.—*C. olivaresi* represents an anomaly among the cis-Andean populations of the *mellisugus* complex: its characters are sharply discordant with the general trends of variation over this broad area. Although large size is a character shared by another isolated mountain endemic, *duidae* of Venezuela, the differences in color and morphology of the latter relative to the forms occurring elsewhere in southern and southeastern Venezuela, *caribaeus* and particularly *subfurcatus,* are differences of degree only: there seems little reason to doubt that *duidae* is but a derivative of one or the other (apparently neither has been recorded from the adjacent lowlands), and there is little reason to suspect that it is reproductively isolated from them (Zimmer and Phelps 1952). In fact, *duidae* was not considered by Mayr and Phelps (1967), although it was recognized as distinct by Meyer de Schauensee and Phelps (1978). The case of *olivaresi* is clearly not comparable to that of *duidae*: it is certainly not an isolated derivative of *napensis* (or any other cis-Andean form). The many points of resemblance to *gibsoni* (bill color, the dull crown of the males, and the rectrix color of the females) suggest that the origins of *olivaresi* might lie with that form, at least in part. At the present time, the ranges of *olivaresi* and *gibsoni* are separated by at least 300 km of forested lowlands and foothills, which constitute unsuitable habitat for both forms which are evidently adapted to dry or edaphically scrubby habitats (and which are inhabited, at least at present, by *napensis*). It is likely that the eastern foothills of the Andes in southeastern Colombia represented a humid enclave or "forest refugium" through Pliocene-Pleistocene times (Haffer 1974, 1985), such that the range of *gibsoni* has probably never included or approached the Sierra de Chiribiquete. A more likely scenario is for one or a few individuals of the ancestral population of *gibsoni* to have dispersed across the forested lowlands to Chiribiquete, perhaps during a dry period in the Pliocene or early Pleistocene. During such a period, the low passes south and west of the Sierra de la Macarena might well have supported a more xeric, scrubby, vegetation suitable for *gibsoni,* facilitating its arrival on the eastern slope of the Andes. Consisting of sandstones of Permian age or earlier, the Sierra de Chiribiquete antedates at least the final uplift of the Andes (cf Galvis, in Estrada and Fuertes 1993), and would have been available for colonization by forms adapted to xeric or open habitats throughout the latter part of the Cenozoic. The final population of *Chlorostilbon* to colonize the Sierra de Chiribiquete might even have been the result of hybridization of the newly arrived *gibsoni*-type birds with the form of *mellisugus* already present in the adjoining areas. At least, this would provide

a tentative explanation for the *mellisugus*-like characters of *olivaresi* (very shallowly forked tail and blue breast of the males). Once established, this population of possibly hybrid origin might well have developed large size in the process of adapting to its peculiar insular habitat. Large size is a feature of some island populations (cf Grant 1965) including those of *Chlorostilbon* (cf Ridgway 1911, Howell 1993), and the large size of *duidae* may represent a result of the same processes, albeit at an earlier and more incomplete stage. A possibly analogous case of presumptive hybrid origin of a currently stable and well-differentiated form among the white-eyes of Reunion Island has been discussed by Gill (1973). Genetic studies in the *mellisugus* complex would assuredly shed light on the origins of *olivaresi,* and might help to resolve several other questions regarding geographical variation and species limits in the complex. In any case, by both biological and phylogenetic criteria, *olivaresi* appears as entitled to separate (allo)species status as does any other form within the entire *mellisugus* complex.

Among the avifauna of the Sierra de Chiribiquete, *C. olivaresi* is also an anomaly. Virtually all of the species of the upper levels of the Sierra whose subspecific allocations could be determined, belong to forms whose distributions include the Llanos, the Orinoco region, and/or the savannas of eastern Vaupés and adjacent Brazil, rather than the Amazonian lowlands and Andean foothills to the west and south (Stiles et al. 1995). The lack of differentiation of these forms suggests a vicariance pattern, probably a relict of more a continuous distribution of savanna or scrub-adapted birds during the dry periods of the Pleistocene. The present isolation of these birds from their relatives to the north and east probably dates back no more than 15,000–20,000 years, much too short a time to have permitted significant differentiation among birds of the Amazon drainage (Capparella 1988).

Interestingly, one other species of Chiribiquete appears to have dispersed from the xeric upper Magdalena Valley rather than having its affinities with forms to the north and east. This species, *Hemitriccus margaritaceiventer,* also appears to have differentiated in Chiribiquete from its putative ancestral population in the Magdalena Valley, although to a much lesser extent. This population clearly represents a distinct subspecies of *margaritaceiventer* (Stiles, unpubl. data), probably of more recent origin than *C. olivaresi.* In general terms, the Chiribiquete avifauna is basically a relict of a formerly more continuous Orinoquian avifauna upon which is superimposed a small number of forms that have dispersed from similar habitats to the west, at different periods of the geological past (cf Mayr and Phelps 1967). The most distinctive, and probably the oldest, of

these forms is undoubtedly the Chiribiquete Emerald, *Chlorostilbon olivaresi.*

AN OVERVIEW OF THE *C. MELLISUGUS* COMPLEX

The most recent treatment of this complex as a whole is that by Sibley and Monroe (1990). These authors consider as allospecies of the *mellisugus* superspecies *canivetii* of México and northern Central America, *assimilis* of southern Costa Rica and western Panama, and *mellisugus* (including *pumilus* and *melanorhynchus*) of northern South America, while excluding *gibsoni* (including *chrysogaster* and *nitens*). This represents the opposite extreme from the broad treatment of Zimmer (1950) who considered all these forms as subspecies of *mellisugus.* Especially in view of the characters of *olivaresi,* which combines certain features of both *gibsoni* and the *mellisugus* group, I would agree with Zimmer that all of these forms are representatives of a common stock. In particular, I see no justification for including the *canivetii* group while excluding *gibsoni* from this complex: they share characters, such as the red lower mandible and deeply forked tail of the males, and extensive gray bases and broad white tips to the lateral rectrices of females (Zimmer 1950). These features could well represent parallel adaptations to more open, seasonal habitats than are occupied by neighboring forms.

In general, I feel that too little attention has been paid to the ecology of these hummingbirds—in particular, the range of elevations and humidity conditions occupied by each form. Although all members of the group prefer open, brushy habitats, so far as known, there are a number of differences that could have bearing on their status. For instance, *pumilus* appears to be primarily a bird of humid foothills, entering well into the subtropical zone where it has been recorded to elevations of 2000 m or more (Hilty and Brown 1986; pers. obs.); the same evidently is true of *melanorhynchus* (Zimmer 1950). The preferred habitat of *gibsoni* appears to be in hotter, drier areas; it occupies the floor of the middle and upper Magdalena Valley, up to ca 2000 m or more in dry valleys, mainly on the western side; *chrysogaster* and *nitens* are mainly or exclusively lowland forms, with the latter occupying the driest areas along the northern coast (Meyer de Schauensee 1948–1952). Also occurring primarily in the lowlands east of the Andes are *caribaeus* (probably throughout the Llanos) and *napensis* in more humid areas farther south, apparently largely in areas of riverine scrub. *Subfurcatus,* by contrast, occurs mostly above 1000 m in the Gran Sabana and tepuis of eastern and southeastern Venezuela and adjacent Brazil and Guyana (Meyer de Schauensee and Phelps 1978); *duidae* is evidently isolated at similar elevations on Cenro Duida (Zimmer and Phelps 1952). Different habitat preferences may help to

promote or reinforce reproductive isolation of different forms where they meet, as perhaps is the case between *pumilus* and *gibsoni* on the western side of the Magdalena Valley. This would likely be the case for *napensis* and *olivaresi,* which appear restricted to the upper elevation *Bonnetia* scrub of the Sierra de Chiribiquete. A detailed study of the displays of these hummingbirds (cf Stiles 1983) might also help to clarify species limits.

On present evidence, I recommend that the relationships of these forms are best expressed by considering the *mellisugus* complex to comprise a single (*mellisugus*) superspecies. In South America, the forms *melanorhynchus* (including *pumilus*), *gibsoni* (including *chrysogaster* and *nitens*), *olivaresi,* and *mellisugus* (including *caribaeus, napensis, phaeopygos, subfurcatus, duidae,* and one or more races in eastern South America beyond the scope of this study; see Zimmer 1950) should be considered allospecies within this superspecies.

In this connection, an interesting analysis of the northern forms of the *mellisugus* complex has recently appeared (Howell 1993). Using arguments similar to those employed here, Howell has presented strong evidence for recognizing *auriceps* of western Mexico and *forficatus* of Cozumel Island, as distinct species. He also advocates recognizing *salvini* of northern Central America as distinct from *canivetii* of southeastern Mexico and extreme western Guatemala (considering the two to comprise a superspecies). In the latter case, however, depth of tail fork (in both sexes) appears to be the only reasonably clear-cut difference. This difference is on the same order of magnitude as that between *caribaeus* and *napensis* (in fact, the mean ratio of the relative tail forks of males of the latter two forms is ca 2.19, whereas the corresponding mean ratio for *canivetii* and *salvini* is only 1.30). The differences in patterns of the rectrices cited by Howell between the two forms (cf his fig. 1) are of a magnitude that, in my experience, could be subsumed by individual variation. In the absence of a more detailed analysis of geographic variation within each form, I am hesitant to follow Howell (1993) in separating these forms at the species level. For the present, I prefer to adopt a more conservative species criterion and consider *canivetii* and *osberti* (the form of *salvini* in question) as only subspecifically distinct, particularly as there does not appear to be any significant ecological difference between them; this is also more consistent with species criteria in the *mellisugus* complex as a whole (contra Howell 1993). This problem clearly merits further study. Also, in keeping with the mosaic pattern of variation in this complex as discussed here, I consider *auriceps* and *forficatus* as allospecies of the *mellisugus* superspecies, rather than as species apart.

I should note here that I had previously (Stiles and Skutch 1989) ques-

tioned the distinctness of *assimilis* from *canivetii,* based upon apparently intermediate birds that I had observed and trapped (but in most cases not collected) along the Pacific coast of southcentral Costa Rica. While widespread hybridization and introgression does occur between Hoffmann's Woodpeckers *Melanerpes hoffmanni* of northwestern Costa Rica and Red-crowned Woodpeckers (*M. rubrucapillus*) of the southern Pacific area following deforestation (cf Stiles and Skutch 1989; various specimens), I now feel that the evidence for the same in *Chlorostilbon* is still too weak to justify lumping *assimilis* and *canivetii* and recommend further study of this problem. For the present, it seems best to follow current practice (A.O.U. 1983, Sibley and Monroe 1990) in considering these forms to be allospecies; indeed, a limited zone of hybridization would not be inconsistent with this interpretation.

In conclusion, I recommend that the "*mellisugus* complex" be recognized as a single superspecies rather than being divided into a mixture of separate species and superspecies, some with disjunct distributions. From Mexico to northern South America, I recommend recognition of the following allospecies: *auriceps, forficatus, canivetii, assimilis, melanorhynchus, gibsoni, olivaresi,* and *mellisugus.* Together, the members of the *mellisugus* superspecies show a fascinating pattern of allopatric distributions and mosaic geographical variation that bespeaks a complex evolutionary history fully in keeping with the complicated geological history of Central America and northern South America during the latter part of the Cenozoic. These hummingbirds would seem to comprise a most fruitful group for further genetic, phylogenetic, and biogeographical studies.

ACKNOWLEDGMENTS

For logistic and financial support during the expedition to the Sierra de Chiribiquete, I am grateful to the Instituto de Cooperación Técnica of Spain, the Instituto de Ciencias Naturales, and INDERENA. For help and companionship in the field, I thank José Luis Tellería, Mario Díaz, Bernardo Ortiz, Augusto Repizzo, and all the other members of our expedition; the surgical expertise of Carlos Castaño was particularly appreciated. Diego Silva and Tomas Walschburger of the Fundación Puerto Rastrojo kindly shared with me their observations from the Río Mesay area. The following kindly provided access to specimens of *Chlorostilbon* in their care: Hno. Roque Casallas of the Museo de La Salle, Bogotá; Hernando Chiriví and Jorge Morales of INDERENA-UNIFEM; and Hno. Marco A. Serna of the Museo del Colegio de San José, Medellín. I am grateful to M. Marín for providing measurements of specimens in the Louisiana State Museum of Natural Science. Arturo Rodríguez contributed valuable curatorial assistance in the Instituto de Ciencias Naturales. S. N. G. Howell and M. Robbins provided useful comments on the manuscript.

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COLOR PLATE

Publication of the frontispiece painting has been made possible by an endowment established by George Miksch Sutton.

Wilson Bull., 108(1), 1996, pp. 28–35

REPRODUCTION AND MOVEMENTS OF MOUNTAIN PLOVERS BREEDING IN COLORADO

Fritz L. Knopf and Jeffery R. Rupert

Abstract.—North American populations of Mountain Plovers (*Charadrius montanus*) have declined 63% since 1966. Using radiotelemetry, we monitored plover nesting and brood rearing during the 1993 and 1994 breeding seasons in Weld County, Colorado. Our objectives were to extend preliminary breeding studies of 1992 (Miller and Knopf 1993) and to determine the minimum area required for successful reproduction by this species. Plovers began arriving on the breeding grounds in mid-March. Due to a high incidence of predation, eggs hatched in only nine of 34 (26%) nests in 1993 and in 20 of 54 (37%) nests in 1994. Daily survival rates of chicks were 0.957 (442 telemetry days, 44 chicks) and 0.951 (610 telemetry days, 42 chicks) each year, respectively. Plover broods moved an average 337 ± 46.5 m/day (N = 30) and 298 ± 41.9 m/day (N = 14) in 1993 and 1994 (t = 1.10, P = 0.27), respectively. Plovers that raised chicks to fledging used between 28 and 91 ha, averaging 56.6 ± 21.5 ha. Daily movement rates (t = 0.7, P = 0.48) and total area used (t = 1.4, P = 0.17) were similar between broods where ≥ one chick fledged and broods from which no chicks fledged. Success of plovers in raising chicks appeared related either to overall fox activity in the area or to how effectively the adult detected and distracted foxes. Most plovers left the breeding grounds in mid-to-late July, four months after arrival. Population declines of Mountain Plovers appear independent of any recent landscape fragmentation within this breeding stronghold of the species. *Received 10 May 1995, accepted 1 Oct. 1995.*

North American Mountain Plover (*Charadrius montanus*) populations declined 63% between 1966 and 1991 (Knopf 1994) and the decline has continued through 1993 (Knopf, in press). This species nests across the western Great Plains and eastern Colorado Plateau region, with the breeding stronghold being in Weld County, Colorado (Graul and Webster 1976). Mountain Plover nests are located in microsites of native shortgrass prairie dominated by blue grama (*Bouteloua gracilis*) with 30% or more of the area being bare ground (Knopf and Miller 1994; Knopf and Rupert 1996). A female plover lays a clutch for the male to incubate then a second clutch for herself (Graul 1973). The precocial chicks receive uniparental care and move up to 800 m from the nest shortly after hatching (Graul 1975). Brood-rearing habitat is described as areas with forbs or objects such as fence posts where chicks can find shade to avoid midday heat (Graul 1975).

In this study, we used radiotelemetry to monitor movements and determine the area requirements of Mountain Plovers during the breeding season. We also provide information on nest success and chick survival to supplement preliminary findings of Miller and Knopf (1993) in 1992.

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We interpret our findings relative to conservation of this rapidly declining species.

METHODS

We studied Mountain Plovers during the 1993 and 1994 breeding seasons on the Pawnee National Grassland (PNG), a 781-km² shortgrass prairie. Graul (1973) summarized the physiography, vegetation, and climate of this region. We concentrated our study on three grazing allotments (Keota, Keota Steer, and Owens) in the vicinity of Keota, Colorado, and on three other allotments (Reno, Sand, and Wildhorse) northwest of Briggsdale, Colorado.

Once a nest was located, we monitored the progression of incubation (29 days) by egg flotation every 3–5 days. During nest monitoring, we drove a vehicle near the nest and, remaining in the vehicle, reached down to remove an egg to avoid spreading human scent in the vicinity. Within 2–4 days before hatching we captured adult birds on nests with a fishing line snare or swing-door box trap made of wire mesh. In 1993, some juveniles from unknown nests were captured by hand and aged per Miller and Knopf (1993) to supplement survival rate data on older chicks.

All birds were banded with a U.S. Fish and Wildlife Service numbered metal band on one leg and colored plastic bands on the other. Plovers (N = 43) were fitted with 1.5–3.0 g radio transmitters with 15 cm antennae (Holohil Ltd., Woodlawn, Ontario, Canada, and Advanced Telemetry Systems, Isanti, Minnesota. Mention of commercial products does not constitute endorsement by the U.S. Government). The transmitter was affixed by applying a light coating of waterproof epoxy adhesive (Titan Corp., Lynnwood, Washington) and sliding it under the upper back feathers. Care was taken not to expose the skin to the epoxy. The transmitter was not visible on the birds and the whip antenna was difficult to see even with binoculars at close (<20 m) distances. Transmitter life was about 90 days, and transmitters remained attached to adult birds until the prebasic molt. Birds were not handled after initial transmitter attachment.

All chicks in monitored nests were color banded on the day of hatching, then never rehandled. We subsequently located broods almost daily at distances up to 1000 m with a TRX-1000 Wildlife Materials Inc. (Carbondale, Illinois) receiver and a hand-held, three-element Yagi antenna. All relocations were from a vehicle, again to avoid spreading human scent. Specific locations of plovers were recorded using the Magellan NAV 5000 Global Positioning System [Magellan Systems Corporation, San Dimas, California]. Position readings were recorded to the nearest hundredth of a minute and only if a satellite geometric quotient registered ≥ 7 on a scale of 1–9. Based upon readings at a known (surveyed) benchmark, accuracy of our specific instrument was calculated at 7.2 ± 1.4 ($\bar{x}$ ± SD) m latitude and 8.4 ± 1.6 m longitude for an area error of ± 60.6 m².

The area used by broods was estimated by superimposing a grid over a map of the study area and counting the number of new cells (10 × 10 m) visited over time. This is an adaptation of the grid-cell home range estimation method first proposed by Siniff and Tester (1965). Whereas discontinuous telemetry data often result in successive locations being several cells apart, we conservatively assumed that birds traveled in a straight line between locations. Thus, area-of-use descriptions are considered to be the minimum (vs actual) area requirements for raising a brood.

RESULTS

Egg/chick survival.—Plovers were first observed on the PNG on 17 March 1993 and 21 March 1994, although the exact date of the first bird

TABLE 1

PRODUCTIVITY AND CHICK SURVIVAL RATES OF MOUNTAIN PLOVERS ON THE PAWNEE NATIONAL GRASSLAND, WELD COUNTY, COLORADO, 1992–1994

Year	No. nests	Nest success (%)	$\bar{x}$ No./Successful nest			Daily survival rate
			Eggs hatched	Chicks fledged	Chicks migrated[a]	
1992[b]	14	50	2.6	1.21	0.74	0.977
1993	34	26	2.4	0.26	0.22	0.957[c]
1994	54	37	2.6	0.35	0.17	0.951[d]

[a] Calculated from average of 18 days that chicks remained on breeding grounds after fledging (Miller and Knopf 1993).
[b] Data from Miller and Knopf (1993).
[c] Based on 442 telemetry days, 44 chicks
[d] Based on 610 telemetry days, 42 chicks.

arriving may have been a day or two earlier. We monitored 34 nests in 1993 and 54 nests in 1994. Three clutches were abandoned each year. In 1993, two clutches were abandoned after being partially predated. The other clutch was abandoned after it had been flooded from 4 to 6 June and then incubated again from 7 to 20 June. In 1994, two clutches were abandoned for unknown reasons. One other was abandoned after being incubated two weeks beyond normal hatching time. Adult plovers from three of the six nesting efforts stayed in the nest area until migrating, whereas the other three left the area within 48 hours and could not be relocated.

Predation rates on both eggs and chicks were high (see Miller and Knopf [1993] for a list of potential predators), and egg and chick survival were low (Table 1). Survival probabilities of the 1994 chicks partitioned into 10-day intervals (day 1–10 = 0.935, 11–20 = 0.957, 21–30 = 0.970, and 31–40 = 0.971) indicate that survival increased with age of the chick. Generally, daily survival rates were only slightly lower than reported for 1992 (Miller and Knopf 1993). However, the lower daily rates resulted in a drastic decline in the number of chicks produced per nesting effort if projected to the time when fledged chicks left the breeding area.

Movement patterns.—We captured and placed transmitters on 17 and 26 adult plovers with broods in 1993 and 1994, respectively. Each brood was tracked until either all members of the brood were killed by a predator or fledged chicks left the nest vicinity. Of adults fitted with transmitters, we obtained prolonged movement and area-of-use data on seven and 14 broods in 1993 and 1994, respectively. An additional 26 chicks were aged and fitted with transmitters in 1993, of which 23 provided usable information. Thus, data were obtained on 30 broods in 1993 and

14 broods in 1994. The average duration of radio-tracking was 10.3 ± 5.2 and 22.9 ± 13.4 days for each brood in 1993 and 1994, respectively.

Based upon 290 telemetry days, plover broods moved an average of 337 ± 46.5 m/day in 1993 (range 61 to 600 m). The 320 telemetry days in 1994 indicated an average move of 298 ± 41.9 m/day (range 85 to 651 m). Distances moved were similar (t = 1.10, P = 0.27, 608 df) between years. Of the 42 broods, 38 moved 100–500 m/day. Of the remaining four broods, two were monitored for only five days and moved <100 m/day. Two others, monitored four days and 13 days, moved 1000 and 1085 m/day, respectively.

Most losses of chicks were to swift foxes (*Vulpes velox*). Average daily movements were similar (t = 0.7, P = 0.48, df = 40) among broods in which all chicks were killed by predators (400 ± 313 m, N = 15) and broods where chicks fledged (340 ± 226 m, N = 27). The total distances moved during the first 10 days after hatching of eggs (when predation rates were highest) were also similar (t = 0.50, P = 0.62, df = 14) between broods in which all chicks were lost and broods where chicks fledged.

Brood-rearing area.—Due to the high rates of predation and some transmitters on older chicks becoming dislodged, we were only able to track six broods from hatching to fledging. The total minimum area used by those six broods ranged from 28 ha to 91 ha and averaged 56.6 ± 21.5 ha. As suspected from the movement data, the average area used on a daily basis by broods where chicks fledged (2.5 ± 1.6 ha, N = 27) vs broods that lost all chicks to predators (3.4 ± 2.4 ha, N = 15) were similar (t = 1.4, P = 0.17, df = 40).

Timing of departure.—At least two adults renested after losing a clutch or brood early in the breeding season (May, early June). One adult whose chicks hatched on 21 May 1993 was located on a second nest 140 m away on 21 June. The transmitter had failed, so knowledge of the fate of the first brood of three chicks is not certain. This bird abandoned its second clutch after it was partially depredated; it remained in the vicinity with other plovers until 14 July when it left the area, returned 26–29 July, then left the area for the season.

This example illustrates the general pattern of flocking and departure from the breeding grounds. A few adult plovers began congregating in flocks in mid-June each year. Fledglings started to appear in these flocks in July. Many adults also were undergoing a prebasic molt at this time, precipitating an increased rate of transmitter loss. Plovers with transmitters began leaving the study areas gradually after mid-June, but a major exodus of plovers occurred mid-late July. Seventeen plovers in 1993 and eight plovers in 1994 which were being located daily were known to have

left the study area between 14 July and 3 August. In 1993, an aerial survey of Weld County from 3 to 9 August confirmed that not one of 17 transmittered birds remained in the vicinity. The few adults (transmittered and untransmittered) that we could find in early August of 1993 all had large chicks incapable of flight.

DISCUSSION

Productivity.—Miller and Knopf (1993) reported that adult survival and productivity on the PNG were similar to historical studies. We recently documented that survival rates of birds wintering in California are also high (Knopf and Rupert 1995). In this study, we recorded daily survival rates of chicks in 1993 and 1994 similar to those reported for 1992. The more intensive efforts described here detected an increasing probability of survival with age of the chick, as reported by Graul (1975). Thus, the 1992 daily survival rate (0.977) was inflated slightly by a high incidence of older chicks being transmittered that year.

An unknown percentage of female plovers lay two clutches, the male incubates the first as the female lays a second clutch for herself (Graul 1973). The incidence of male-incubated clutches may increase with food abundance (Graul 1976). Thus, whereas 0.26 and 0.35 chicks fledged per nest compares poorly with fledging rates of some other North American plovers (Page et al. 1983, Haig and Oring 1988, Prindiville Gaines and Ryan 1988), the actual productivity per pair may be up to twice that value in a given year.

The number of eggs hatched per clutch has remained stable when compared to studies conducted 10 (McCaffery et al. 1984) and 25 (Graul 1975) years earlier. Most reproductive losses were due to fox predation. We believe that the greater losses of nests and chicks to predators in 1993 and 1994 compared to 1992 were attributable indirectly to reduced food resources. Mountain Plover reproductive efforts (Graul 1976), as those of other grassland birds (George et al. 1992), are less successful in years of drought. The two seasons of this study were drought years on the PNG. Grasshoppers are a major food item of both plovers and foxes, and their populations were very low both years. Low grasshopper populations would increase the time spent foraging for both species, thus increasing the probability of eggs and chicks being detected by foxes.

Movement patterns.—Reproductive success of many birds appears to be a tradeoff between acquiring food and risking predation (Martin 1992). From an evolutionary perspective, numerous traits of Mountain Plovers may reduce detection by predators, including the cryptic coloration of chicks and crypsis to avoid detection (Sordahl 1991), two clutches incubated separately by the two adults (Graul 1973), shell removal at hatch-

ing (Graul 1975), rapid movement of chicks away from the nest (Graul 1975), predator distraction displays by adults (McCaffery et al. 1984), and the ability of chicks to fly at only 70% of adult body weight (Miller and Knopf 1993).

Mountain Plovers led hatchlings away from the nest as soon as they were dry. We regularly tracked the directional movement of a brood up to 2 km within two or three days of hatching. Many plovers moved broods to areas of disturbed prairie (Knopf and Rupert 1996) and then remained in those general areas. In contemporary prairie landscapes, such disturbances are either areas frequented for watering and loafing by cattle or fallow agricultural fields. After the initial move, many broods remained in the vicinity of these areas where chicks foraged on small insects.

Area requirements.—This study was precipitated by the conservation need for information on the minimum area necessary for plovers to raise chicks. The minimum area within which a brood was raised was 28 ha. Plovers raised chicks in broadly overlapping areas, with two or three broods sometimes occurring in a general vicinity (such as around a cattle watering tank). Thus, the potential exists for a suitable area to meet the needs for more than one bird to raise chicks successfully.

The movement rates and area-of-use by plovers that successfully raised their chicks to fledge did not differ from those of plovers that lost the entire brood. Swift foxes were often seen hunting during daylight hours (especially after mid-June as pups began eating prey) in addition to night foraging. The eventual success of a plover in raising its chicks appeared to be the result of either the overall fox activity in the immediate area being used by the brood or the effectiveness of the adult plover in detecting and distracting a fox.

Departure from breeding grounds.—Most Mountain Plovers that bred in Weld County left by 1 August each year. Occasional flocks of plovers were seen after early August, with the latest being on 8 October 1993. We assumed the later flocks were of birds moving south from more northerly nesting areas. The first plovers arrive on California wintering grounds in mid-October. The prolonged period of migration to the wintering areas is in sharp contrast to the apparently direct, nonstop flight from California back to Colorado in March (Knopf and Rupert 1995). Plovers spend approximately four months on their Colorado breeding grounds, five months on the California wintering grounds, and three months moving from the former to the latter.

CONCLUSIONS

Miller and Knopf (1993) concluded that recent population declines of Mountain Plovers can be attributed either to long-term declines in repro-

ductive success or to phenomena occurring at nonbreeding areas. The comparatively lower survival rates of chicks observed in 1993 and 1994 support that preliminary conclusion. Although swift fox densities seem high on the PNG, the fox is only locally distributed within the breeding range of the plover. We would not expect, for example, such a high rate of predation in Phillips County, Montana (the second major breeding locale) due to the absence of foxes in that state.

The shortgrass prairie, like many native vegetative associations, has become highly fragmented in the last century. The PNG is no exception, with 781 km^2 occurring in 130 parcels ranging from 16 to 23,895 ha (B. Ladd, pers. commun.). Although some of the smaller PNG parcels are <28 ha, the minimum area required for brood rearing, all are contiguous to private lands that are likewise managed as rangelands. We feel that these private lands also provide suitable Mountain Plover habitat. Thus, we conclude that virtually all relatively flat, grazed shortgrass prairie parcels provide potential habitats for plovers on the PNG. The current decline of the North American Mountain Plover population appears independent of recent fragmentation of landscapes within the native shortgrass prairie of northeastern Colorado, the breeding stronghold (Graul and Webster 1976) of the species.

ACKNOWLEDGMENTS

We thank the U.S. Forest Service, for financial assistance, and personnel of the Rocky Mountain Region, Arapaho-Roosevelt National Forest, and the Pawnee National Grassland District for technical assistance. We are especially grateful to Larry Mullen for administrative support. The Colorado Division of Wildlife conducted aerial reconnaissance, and we specifically thank Jim Dennis for his efforts. Susan Skagen and Tex A. Sordahl provided helpful comments on the manuscript. Clif Knopf provided assistance in the field.

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Wilson Bull., 108(1), 1996, pp. 36–52

TRIGEMINAL REPELLENTS DO NOT PROMOTE CONDITIONED ODOR AVOIDANCE IN EUROPEAN STARLINGS

LARRY CLARK

ABSTRACT.—Birds, and in particular European Starlings (*Sturnus vulgaris*), avoid consumption of fluid and food treated with the natural plant products, methyl anthranilate and o-aminoacetophenone. Avoidance is an unlearned response most likely mediated via chemically sensitive fibers of the trigeminal nerve. The trigeminal nerve codes for chemical irritation and pain. Starlings are not repelled by the odor of the compounds, nor is olfaction important in the avoidance response. Moreover, starlings fail to learn to avoid the odor of the repellents, even after direct oral contact with liquid repellent. While trigeminal irritants can be powerful repellents, the absence of associative learning for these repellents will influence the application strategy for formulation and use. More broadly, the difference in learning abilities associated with trigeminal repellents and those commonly responsible for conditioned avoidance learning have implications for the structure of chemical defenses of fruits and the prevention of untimely frugivory. *Received 24 Feb. 1995, accepted 1 Sept. 1995.*

Nonlethal bird repellents are important components of an integrated wildlife management strategy. Repellents can be used to protect birds from human activities (Clark and Shah 1993) or to minimize damage caused by birds (Mason and Clark 1992). The social emphasis on safe, nonlethal methods to resolve conflicts between humans and birds has resulted in numerous attempts to identify new repellents (Dolbeer 1986, Crocker and Perry 1990, Clark and Shah 1991). However, reported efficacy of nonlethal repellents is highly variable (Mason and Clark 1992). In part, this is due to a misunderstanding about how repellents work. To minimize failure rates in the field, several fundamental questions about mode of action and formation of avoidance response remain to be resolved.

Nonlethal chemical repellents operate via two distinct mechanisms (Zahorik 1976), conditioned avoidance and nonlearned avoidance. In conditioned avoidance learning, birds learn to avoid sensory cues paired with a stimulus that causes illness (Garcia et al. 1966). The magnitude and persistence of the avoidance response depends on the toxic potential of the sickness producing agent and the localization of the illness. Pelchat et al. (1983) found conditioned avoidance was strongest in the rat when

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sickness was localized in the upper region of the small intestine. In birds, ingestion of carbamate insecticides (e.g., methiocarb) and fungicides (e.g., thiram, ziram) causes gastrointestinal sickness. Substances causing sickness have been used to condition birds to avoid tastes (Schuler 1983), odors (Clark and Mason 1987), and visual cues (Mason and Reidinger 1983). In a nonlearned avoidance response, substances possess taste, smell, or irritating qualities that are perceived as unpalatable by birds. Generally, in the quantities ingested, these substances do not cause sickness (Clark and Mason 1993).

Previous studies indicated that acetophenone and anthranilate bird repellents must be present in high concentrations to be effective (Clark et al. 1991). High concentrations of repellents (hundreds to thousands ppm) can be delivered orally, in food or fluid, or to the eye via aerosols. Responsiveness to only high concentrations suggests mediation by the trigeminal system as opposed to olfaction or taste (Walker et al. 1986). Chemically sensitive fibers of the trigeminal nerve mediate response to irritating and painful stimuli (Green et al. 1990). Yet coding for pain or irritation does not necessarily imply tissue damage (Clark 1995).

Common questions are whether the odors of acetophenones and anthranilates are repellent or whether birds can learn to avoid the odor of these repellents. These questions imply avoidance behavior mediated via olfaction and the formation of a conditioned avoidance response. Determining whether avoidance is influenced by olfaction or trigeminal cues is critical to the conceptualization and implementation of delivery strategies of repellents and to the understanding of how birds may respond to natural plant or insect chemical defenses.

The experiments in this paper address these question and are used to argue the point that acetophenone and anthranilate compounds are trigeminal irritants (repellents). As a test of the appropriateness of the experimental paradigm, the effect of short-term water deprivation on subsequent drinking assays was evaluated in Experiment 1. Experiment 2 tested whether naive starlings avoided the odor of a repellent and whether oral contact with a repellent was a sufficiently adverse experience to train starlings to subsequently avoid the odor of a repellent. This experiment also tested the effect of stimulus sequence on the outcome of the drinking assays. Experiment 3 tested the effect of prolonged exposure to orally delivered repellents on the subsequent response to the odor of the repellent. In Experiment 4, the role of olfaction in the mediation of the avoidance response was assessed.

METHODS

Study subjects.—European Starlings (*Sturnus vulgaris*) were decoy-trapped at Sandusky, Ohio, and transported to the laboratory in Philadelphia where they were kept in group

housing until selected for experimentation. Starlings were maintained on chick starter mash (*ad libitum*) supplemented with a vitamin mixture and fresh apples (weekly). Tap water was available continuously, except during testing. Because starlings exhibit a seasonality in their olfactory ability (Clark and Smeraski 1990), all tests were conducted during the spring when starlings have good olfactory acuity and discrimination ability. Starlings were maintained on a constant temperature (23°C), 14:10 h light : dark cycle during their residence in the laboratory.

Test stimuli.—Fluid intake for o-aminoacetophenone (OAP) and methyl anthranilate (MA) was evaluated using standard 6-h one-bottle (no-choice) drinking tests (Clark and Shah 1994). These compounds were selected as representative of nonlethal acetophenone and anthranilate bird repellents. Both compounds are natural plant metabolites that have organoleptic characteristics that humans perceive as a musky/foxy odor for OAP and a grapey odor for MA (Acree et al. 1990). Concentrations selected for testing were based upon water solubility limits of the least soluble compound (MA) and the least practical concentration yielding reliable rejection of treated fluid by most starlings.

Experiment 1: Effects of water deprivation on fluid consumption.—The objectives of the first experiment were to (1) determine the effect of diurnal water deprivation on overnight water consumption and (2) determine the effect of a three-day diurnal water deprivation schedule on post-test water intake. Determining the potential magnitude of the carry-over effect attributable to water deprivation was important for the interpretation of other experiments relating to the effects of chemical repellents. While previous studies showed that the 6-h drinking test used here is not sufficient to cause a severe water deficit in starlings (Clark and Shah 1991), it was decided that a revisitation of these questions was in order.

The experimental design consisted of a standard one-bottle, 6-h assay. On the first day (the pre-test period), 18 birds were randomly assigned to three groups (N = 6/group) and presented with tap water in graduated Richter tubes. The recording period began at 10:00 and ended at 16:00 (hereafter defined as the diurnal test period). The Richter tubes were replaced with a second set of tubes and water was available *ad libitum* through the period 16:00 to lights out at 19:00, throughout the night, and for the period from lights on at 7:00 to 10:00, the start of the next test sequence (hereafter defined as the overnight period). As a precondition for further testing, similarity for average diurnal water consumption among groups was verified using a one-way fixed effects analysis of variance (anova).

On the second day, birds within the groups were presented with one of three randomly assigned treatments. Birds within the control group were presented with tap water. Birds within the second group were presented with a 28 mM solution of o-aminoacetophenone (OAP). Because OAP is a potent bird repellent, it was anticipated that this group would experience voluntary water deprivation by avoiding the treated water (Clark and Shah 1991). Birds within the third group were water deprived by physically excluding them from the Richter tubes. The protocol for recording water consumption for the diurnal and overnight periods followed that described above. Birds retained their water presentation treatment assignments for days three and four, and water intake for the diurnal and overnight periods followed the format described above.

On the fifth day (the post-test period), birds within all three treatment groups were presented with untreated tap water and intake was monitored according to the prescribed protocol.

The first question, "... does diurnal fluid deprivation affect overnight water consumption?", was addressed using a 3 × 3 repeated measures fixed-effect analysis of covariance (ancova). The dependent variable was overnight water consumption. The previous day's diurnal fluid intake was used as a covariate. Because the covariate was measured each day along with the dependent variable, it was treated as a changing covariate, i.e. separate

residuals were calculated for each day. Days were treated as a repeated measure, and group was treated as a between measures effect. Multivariate criteria (Rao R, Wilk's lambda) were used to simultaneously test repeated measures contrasts on adjusted means when there were more than two levels on the repeated measure. This approach is to be preferred because it does not rely on the assumption that the repeated measures are independent. In circumstances where only univariate statistics were estimable, i.e., one degree of freedom, the F statistic was used to assess significance. The latter case was most common in planned comparison of treatment levels by contrasts. All post-hoc tests were analyzed using a Scheffe's test. This and subsequent analyses were carried out using the STATISTICA™ (1994) software packages (MANOVA procedures). This software is particularly suited to repeated measures and other longitudinal designs.

The second question, "... did the intervening treatments affect post-test water intake relative to the pretreatment period?" was addressed using a 2 × 3 repeated measures fixed-effect ANOVA. The dependent variable was diurnal fluid intake, period (pre vs post test) was a within measures (repeated) effect, and group (i.e., water deprivation schedule) was a between measures effect.

Experiment 2: Effects of odor and treatment sequence on water consumption.—Starlings readily form conditioned odor avoidance responses when the unconditional stimulus produces a strong gastrointestinal illness (Clark and Mason 1987). Starlings also avoid some substances upon initial contact, indicating that the avoidance in not learned (Clark and Mason 1993). This latter response indicates a different mechanism for avoidance, one that suggests hedonic attributes (e.g., taste, smell, irritation) form the basis of acceptance or rejection. Clark and Mason termed these compounds sensory repellents. The objectives of this experiment were to (1) determine whether oral and/or nasal exposure to OAP influenced fluid intake, (2) determine whether starlings could learn to avoid the odor of OAP once they had an aversive oral exposure to the substance, and (3) assess whether the order of presentation of OAP in solution or odor influenced the behavioral response.

Thirty-six starlings were randomly assigned to six groups of six birds each. On the first day, birds were tested for baseline water consumption in a standard 6-h drinking test following procedures outlined in Experiment 1. Attached to both sides of the Richter tube sipping port was a 40 mm diameter, opaquely screened polypropylene disk containing a wick saturated with tap water.

During the three-day test period, birds were presented with one of three treatment conditions (Richter tube/wick disk combinations): [w/w] a tap water filled Richter tube and a tap water soaked wick, [o/w] a Richter tube filled with 28 mM OAP solution and tap water soaked wick, and [w/o] a tap water filled Richter tube and an OAP soaked wick. Presentations of the Richter tube/wick combinations to experimental cohorts were established according to two possible Latin square designs (Table 1). On the fifth day (post-treatment period), all birds were presented with the control tube/wick pairing (w/w). Diurnal and overnight fluid intake were monitored following procedures outlined in Experiment 1.

Data were analyzed using a fixed-effects 3 × 3 × 6 nested ANOVA design with repeated measures. Diurnal fluid intake was the dependent variable and day was a repeated measure with three levels. Sequence (two levels) and group (six levels) were between measures effects, with group nested within sequence (Table 1). To test whether the context of stimulus presentation is important for repellency, contrasts between w/w and o/w, and w/w and w/o were made for the first day of testing. These comparisons addressed the question of whether OAP in solution (where olfactory, gustatory, and trigeminal systems may influence responding) or whether OAP as an odor stimulus (where olfactory and trigeminal systems may influence responding) were important in the formation of an avoidance response. By considering only the first day of testing, these comparisons controlled for possible learning

TABLE 1

LATINIZED DESIGNS FOR THE PRESENTATION ORDER OF TREATMENTS[a]

	Design 1				Design 2		
Day	1	2	3	Day	1	2	3
Group 1	w/w	o/w	w/o	Group 4	w/o	o/w	w/w
2	o/w	w/o	w/w	5	o/w	w/w	w/o
3	w/o	w/w	o/w	6	w/w	w/o	o/w

[a] Experimental codes are: (w/w) tap water presented in the Richter tube with blank odor disks on either side of the drinking port; (o/w) 28 mM OAP solution in the Richter tube with blank odor disks on either side of the drinking port; (w/o) water presented in the Richter tube with saturated OAP wicks in the odor disks on either side of the drinking port.

effects while considering whether repellency is mediated via nasal/ocular (i.e., volatile) or oral/nasal/ocular (i.e., contact and volatile) mechanisms. Similar contrast analyses comparing w/w to w/o were performed for days two and three. These tests allowed for the possibility of learning while addressing the question whether consumption for birds exposed to odor differed from that of the control condition.

OAP is a good sensory repellent when delivered orally. However, can oral presentation of OAP be used to condition birds to avoid the odor of OAP? This question was addressed by inspection of contrasts of the day × treatment interaction term. Intake for birds presented with treatment levels w/w and w/o on day 2 were compared for those birds presented with o/w on day 1, i.e., the putative training day. The overall sequence effect throughout the test was determined by consideration of the main effect and by inspection of post hoc differences among means grouped by treatment category using the Scheffe's test.

Experiment 3: The conditioned odor avoidance response.—In the absence of water deprivation effects (Experiment 1), sequence effects (Experiment 2), and an apparent inability for short exposure to orally delivered OAP to act as an unconditional stimulus (Experiment 2), the length of time starlings were orally exposed to a chemical repellent was increased to determine whether a conditioned avoidance response towards odor could be attained.

Separate experiments on two bird repellents were carried out, and the experimental design of these tests was as follows. Starlings were tested serially for fluid intake in a standard no-choice (one-bottle) 6-h drinking assay. On the first day, eighteen starlings were drawn at random from the group housing pool, randomly assigned to one of two groups (N = 9/group) and pre-test water consumption was monitored according to methods described in Experiment 1. Attached to both sides of the Richter tube sipping port was a 40 mm diameter, opaquely screened polypropylene disk containing a wick saturated with tap water (w/w, following the nomenclature convention in Experiment 2).

For each of three successive days (2–4), starlings within groups were presented with Richter tubes containing a 28 mM solution of a sensory repellent (OAP or MA) and diurnal fluid intake was monitored as described above (Experiment 1). Attached to both sides of the Richter tube sipping port was a wick saturated with tap water (o/w). The strong odor derived from the repellent emanated from the drinking port of the Richter tube, i.e., repellent solution.

On the fifth and sixth day, starlings were presented with Richter tubes containing tap water and fluid intake was monitored as above. During this period the wick inside the disks was saturated with repellent (w/o). Thus, the strong odor of the repellent was present in the apparatus but did not originate from the solution.

Data were analyzed using a fixed effects one-way ANOVA with repeated measures on

days/treatment effect. The confounding of day and treatment on water intake was considered unimportant. Thus, in the absence of carryover effects due to diurnal water deprivation (Clark and Shah 1991, Experiment 1), any day/treatment effect was to be interpreted primarily as a treatment effect. In addition to the day/treatment effect, a single *a priori* planned comparison was made using contrasts. The w/w condition on day 1 was compared to the w/o condition (days 5–6) as an assessment for the formation of a conditioned odor avoidance response. The results for the OAP and MA tests were analyzed separately.

Experiment 4: The role of olfaction in the avoidance response.—Odors can stimulate the olfactory system, but they can also gain access to chemically sensitive receptors of the trigeminal system via the mouth, nose, or eye. Thus, avoidance of an odor might be based upon its unpleasant smell or on its irritating/painful properties.

The object of Experiment 4 was to determine the influence of olfaction on fluid intake when odor was present in the fluid to be consumed. The experimental design was as follows. Starlings were tested for fluid intake in a standard no-choice (one-bottle) six hour drinking assay. The experiment comprised two surgical conditions (Surgery effect: sham or bilateral olfactory nerve cut [BONC]), two repellent concentration conditions (Concentration/Group effect: 14 mM and 28 mM), and two test periods (day/treatment effect: pretreatment = water presentation and treatment = chemical repellent presentation). The confounding of time and treatment was considered to be unimportant (Experiment 1), and any differences were assumed to be attributable to the presence of repellent. Data were analyzed using a fixed effects, 3-way analysis of variance with repeated measures on the day/treatment effect.

Sixteen starlings were selected at random from the group housing pool and randomly assigned so that eight received a BONC and the other eight received a sham surgery. Starlings were anesthetized with choral hydrate/penabarbitol at a dose of 2 ml/kg, intraperitoneally and placed in a head-holder. Surgery for BONC and sham treatments followed procedures outlined in Clark and Mason (1987). Following surgery, starlings were housed individually in cages (61 × 36 × 41 cm). Two weeks following surgery, birds were adapted to experimental conditions. The two-week latency period was estimated to provide sufficient time for degeneration of olfactory afferents into the olfactory bulb, yet not sufficiently long to allow olfactory nerve regeneration (Wenzel and Salzman 1968). Following adaptation one half of the birds within the BONC and sham surgery treatments was randomly assigned to concentration groups, resulting in four birds per experimental cell. On the first day of testing (pretreatment period), beginning at 09:30 h, consumption of tap water was recorded every 2 h for the next 6 h. On the second day, starlings were presented with their preassigned concentration of OAP and fluid intake was monitored every 2 h for the next 6 h. Fluid was presented in 120 ml graduated Richter tubes. Starlings were visually isolated from one another as well as from the contents of the Richter tubes. After five days rest, the same birds used in the above experiment were re-randomized with respect to concentration group assignment and tested with MA using the above protocol.

At the end of the experiments, birds were killed with pentobarbital and sequentially perfused with physiological saline, 10% formalin and a 10% formalin and 30% sucrose mixture. Brains were removed and the effect of the nerve section on olfactory bulb structure was evaluated in a double blind sequence. Briefly, the anterior tips of the hemispheres (containing the olfactory bulbs) were cut into 50 μm slices. Every fifth slice was stained with Nissl stain to highlight the outline of the glomeruli. The observer (familiar with normal histological structure of avian olfactory bulbs) categorized the coded histological series as being either in a degenerative state or normal. Concordance of the observer's scoring and the surgical status were compared using a chi-square analysis. Degeneration of the glomerular structure was taken as evidence for lack of olfactory nerve input into the olfactory bulb (Wenzel and Salzman 1968).

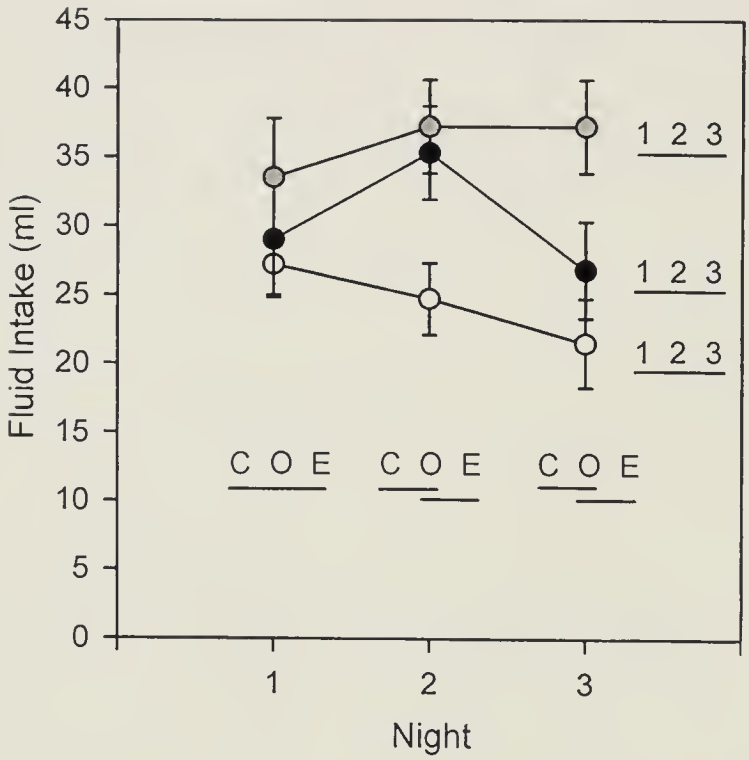

FIG. 1. Average overnight water consumption as a function of time and water deprivation schedule (Experiment 1). Open circles = control group (C); solid circles = OAP group (O); Shaded circles = water excluded group (E). Horizontal bars depict statistically similar water consumption (Scheffe's test, $P > 0.05$). Letters compare average intake across treatment categories within a single night. Numerals compare average intake across nights within a single treatment category. Vertical capped bars depict ± one standard error.

Zinc sulfate ($ZnSO_4$) also has been used to render birds anosmic. However, because $ZnSO_4$ strips away the olfactory epithelium (Burd 1993), it may also affect epithelial layers containing trigeminal free nerve endings. There are no data on this latter point. Because of this uncertainty, surgical manipulation of the olfactory nerve was deemed to be the best way to determine the role of olfaction in the avoidance response.

Directly eliminating trigeminal input is not feasible. In birds, only the ophthalmic branch of the trigeminal nerve (OBTN) is easily accessible for denervation studies (Getty 1975). Manipulation of the maxillary and mandibular branches would require too much destruction of bone and muscle tissue. All three branches could be eliminated at the Gasserian ganglion located in the eye orbit, but this would require permanent blinding of the bird.

RESULTS

Experiment 1: Effects of water deprivation on fluid consumption.—The overnight fluid intake for the treatment groups, adjusted for the covariate of diurnal fluid intake, differed across days (Rao $r = 4.55$, $P < 0.007$). The post-hoc analysis indicated that the overnight water consumption within treatment groups was similar across nights (Fig. 1). However, water consumption differed among treatments within nights. On the first night, all birds consumed similar amounts of water. On the second and third

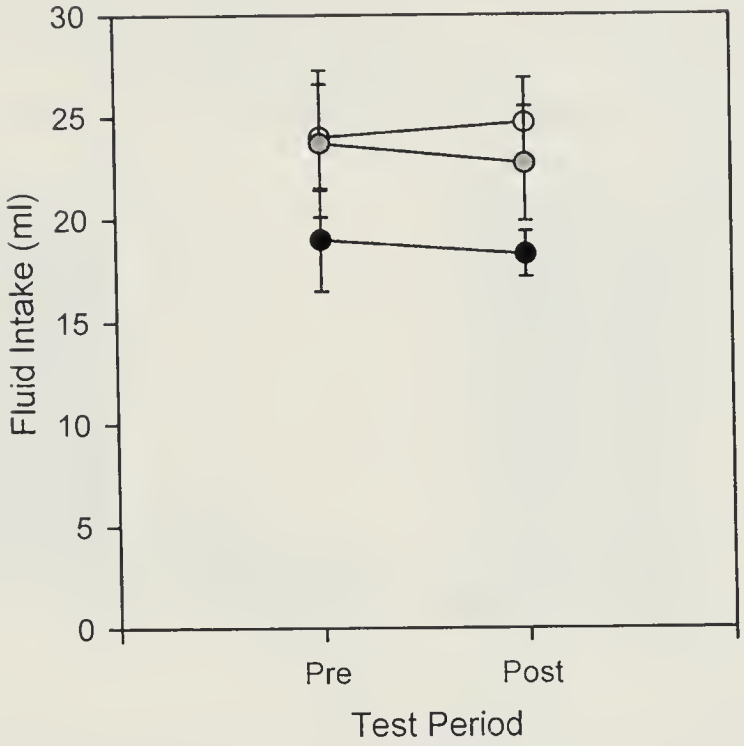

FIG. 2. Average diurnal water consumption as a function of treatment group and time (Experiment 1). Open circles = control group; solid circles = OAP group; shaded circles = water excluded group). Vertical capped bars depict ± one standard error.

nights the control birds drank less water than the birds that were physically excluded from water during the day. Overnight consumption for birds presented with OAP did not differ from the other two experimental groups. There was an inverse, albeit nonsignificant ($P < 0.099$), relationship between daytime fluid intake and subsequent overnight water consumption (Fig. 1). Birds experiencing fluid deprivation by exclusion tended to have the highest overnight water intake (36.0 ml ± 3.7 SE), followed by birds experiencing deprivation by repellency (30.4 ml ± 3.6 SE). Control birds that had *ad libitum* access to water showed the lowest overnight water consumption (24.3 ml ± 2.7 SE). Treatment category did not appear to affect baseline diurnal water consumption immediately following the tests (Fig. 2). There were no group ($P < 0.453$), test period ($P < 0.889$), or interaction ($P < 0.362$) effects.

Experiment 2.—The context of the stimulus is important for repellency. With no prior experience, starlings presented with OAP in solution consumed less fluid than the controls ($F = 94.86$, df = 1,30, $P < 0.001$). This observation stands in contrast to the similarity of diurnal fluid intake for the controls (w/w) and birds presented with water and OAP odor (w/o) ($P < 0.45$). Thus, odor alone is not a sufficiently strong stimulus to

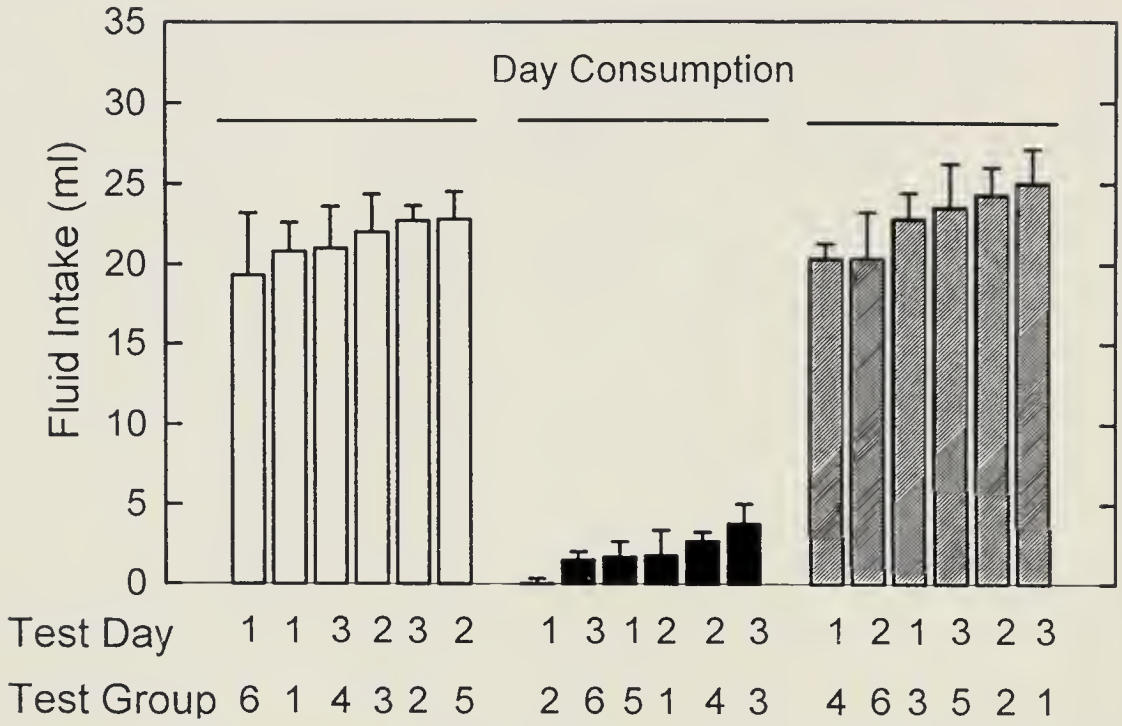

FIG. 3. Average, diurnal fluid intake as a function of time and treatment (Experiment 2). Birds in the control group (w/w, open bars) were presented with tap water in the drinking tubes and disks contained water soaked wicks, birds in the OAP group (o/w, solid bars) were presented with a 28 mM solution of o-aminoacetophenone in the drinking tubes and disks contained water soaked wicks, birds in the odor group (w/o, hatched bars) were presented with water filled drinking tubes and wick soaked in OAP. Average intake is ranked within treatment type and nonsignificant ($P > 0.05$) differences among means are depicted by the horizontal bar. Test Day and Test Group are the column and row label designations of the two Latinized presentation designs described in Table 1. Vertical capped bars depict one standard error.

result in avoidance. This pattern persists even for experienced birds. On days two and three the comparison w/w to w/o indicates similar levels of fluid intake ($P < 0.966$ and 0.21, respectively), irrespective of the previous treatment exposure. The lack of an overall test sequence ($P < 0.305$) or day ($P < 0.121$) effect on diurnal fluid intake is apparent in Fig. 3.

Starlings do not readily acquire a conditioned avoidance response to the odor of OAP when orally delivered OAP is used as the unconditional stimulus. Comparison by contrasts of w/w to w/o on the second day of testing when both groups received o/w on the first day failed to uncover differences in fluid consumption ($P < 0.591$).

As was the case for Experiment 1, the intervening three day treatment schedule had no effect on baseline water consumption. There were no group, day or interaction effects for the pre-test vs post-test comparison

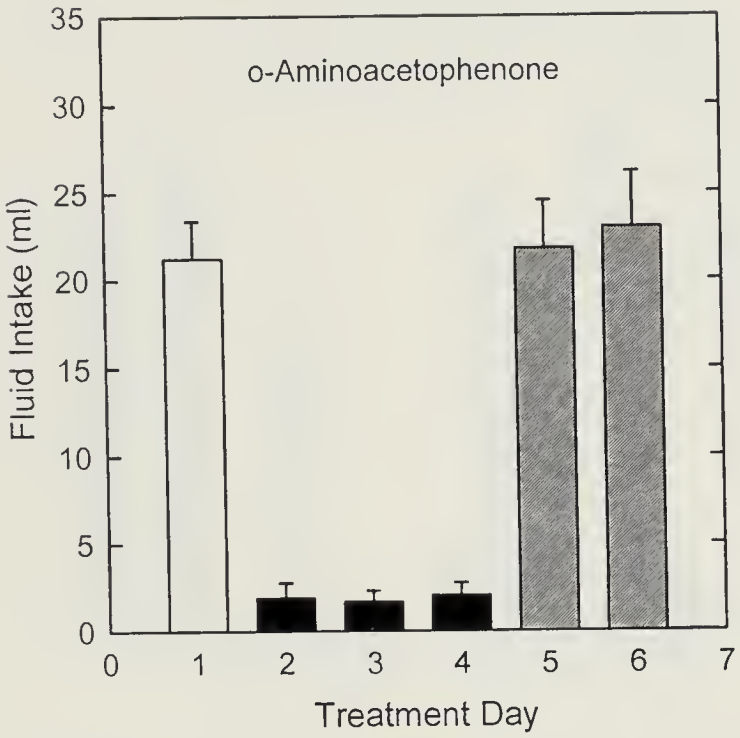

FIG. 4. Average fluid intake for OAP as a function of time and solution treatment (Experiment 3). The left most open bar depicts intake of tap water paired with a water soaked wick in the odor disc (w/w). The middle solid bars depict fluid intake of a 28 mM o-aminoacetophenone (OAP) solution paired with a water soaked wick in the odor disc (o/w). The right most hatched bars depict fluid intake of tap water paired with an OAP soaked wick in the odor disc (w/o). Vertical capped bars depict one standard error.

of diurnal water consumption ($P < 0.351$, < 0.434, < 0.674, respectively).

Experiment 3: The conditioned odor avoidance response.—There were significant day/treatment effects for both the OAP and MA tests (Rao's $r = 9.56$, $P < 0.024$ and $r = 12.48$, $P < 0.15$, respectively). The planned comparisons indicated that fluid consumption was similar for the w/w and w/o treatment conditions for both OAP ($P < 0.72$, Fig. 4) and MA ($P < 0.87$, Fig. 5). Thus, three days exposure to orally administered repellent was not sufficient for the formation of a conditioned avoidance response to that odor.

Experiment 4: The role of olfaction. There was a strong day/treatment effect for OAP ($F = 74.57$, df = 1,12, $P < 0.001$), showing that overall fluid intake was suppressed when the starlings were presented with either 28 or 14 mM OAP solutions (Fig. 6). None of the other effects achieved probability levels less than $P = 0.15$. The planned comparisons between sham-OAP and BONC-OAP within each concentration showed that surgery had no effect on avoidance of OAP ($P < 0.619$, 0.62, respectively).

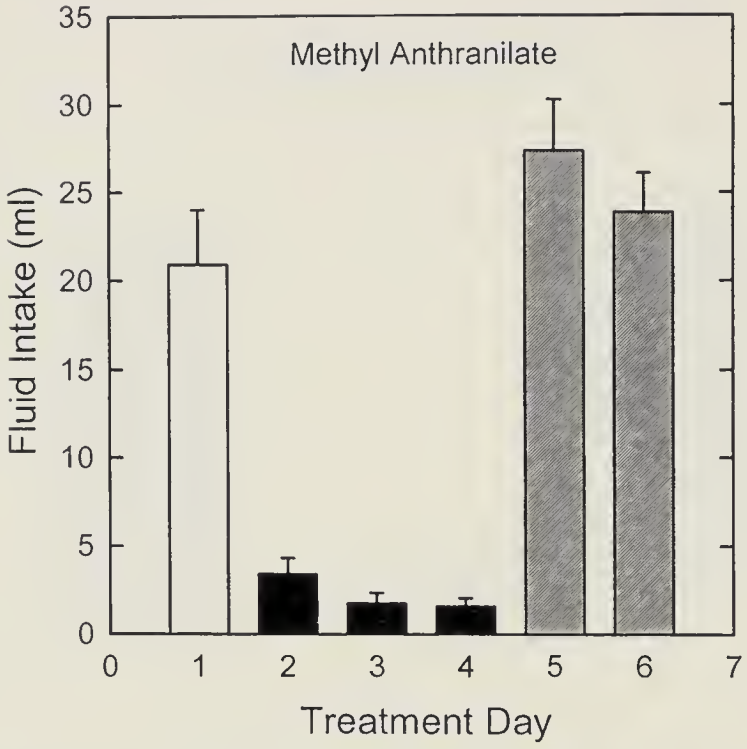

FIG. 5. Average fluid intake for MA as a function of time and solution treatment (Experiment 3). The left most open bar depicts intake of tap water paired with a water soaked wick in the odor disc (w/w). The middle solid bars depict fluid intake of a 28 mM methyl anthranilate (MA) solution paired with a water soaked wick in the odor disc (o/w). The right most hatched bars depicted fluid intake of tap water paired with a MA soaked wick in the odor disc (w/o). Vertical capped bars depict one standard error.

Similar consumption patterns were observed for the MA trials. There was a strong period effect for MA ($F = 83.14$, df = 1,12, $P < 0.001$), showing that fluid intake was suppressed across all surgery and concentration levels when starlings were presented with MA solutions (Fig. 7). No other effect achieved probability levels less than $P = 0.22$. The planned comparisons between sham-MA and BONC-MA within each concentration showed that surgery had no effect on avoidance of MA ($P < 0.215$, 0.399, respectively).

Post-mortem visual inspection of the glomerular layer of sham surgery birds showed a diffuse pattern seen in normal starlings, typical for the spring breeding season. In contrast, BONC birds showed a complete break down of the glomerular structure. The birds were euthanized 20–25 days after surgery. The observer scoring the slides, but blind to the experimental identity, categorized all BONC tissue as having degenerative glomeruli (N = 8) and all SHAM tissue as being normal (N = 8) ($\chi^2 = 16.0$, df = 1, $P < 0.001$).

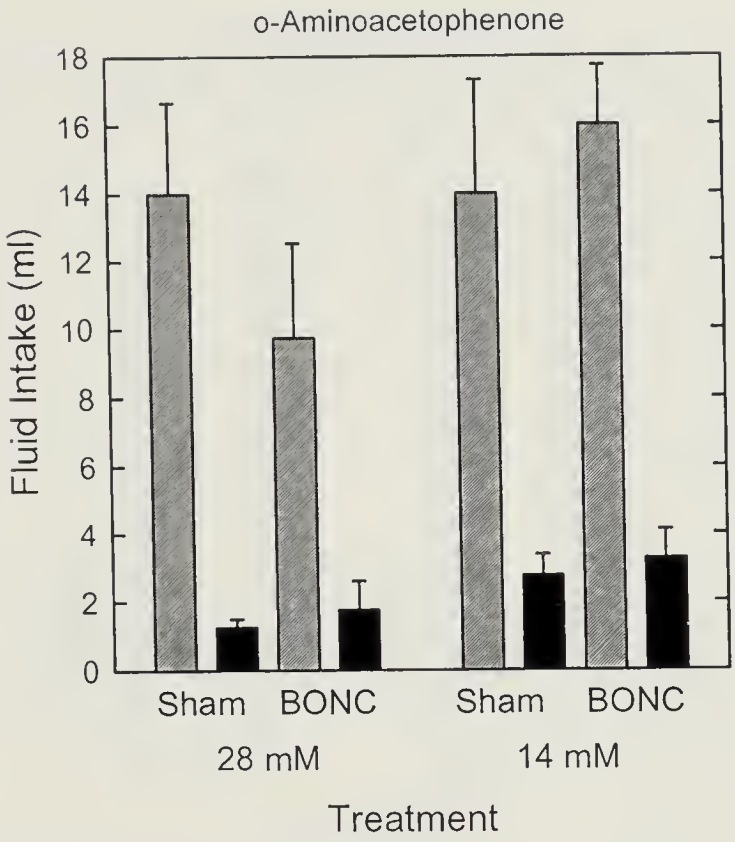

FIG. 6. Average fluid intake for OAP as a function of a solution's molar concentration, surgery and treatment period. Starlings were presented with tap water during the pretreatment period (hatched bars) and an OAP solution during the treatment period (solid bars). Capped vertical bars depict one standard error.

DISCUSSION

When deprived of water during the day, starlings drank more water than normal during the overnight recovery period. However, there was no difference between pre- and post-test diurnal water consumption, irrespective of the experimental water deprivation schedule (Experiment 1). Together these data suggest that the effects of short-term water deprivation are ameliorated during the 18-h recovery period. This lack of carryover, i.e., day effect, is consistent with previously reported results for similar experiments (Clark and Shah 1991).

The use of the two Latinized square treatment presentation sequences allowed a detailed analysis of the influence of delivery route on the avoidance response (Experiment 2). Naive starlings that were exposed to only the odor of OAP did not avoid the drinking apparatus, suggesting that the odor of OAP was not repellent. Only when OAP was allowed to come in contact with the mouth did starlings show an avoidance response.

Starlings failed to avoid the odor of OAP even after they had come in

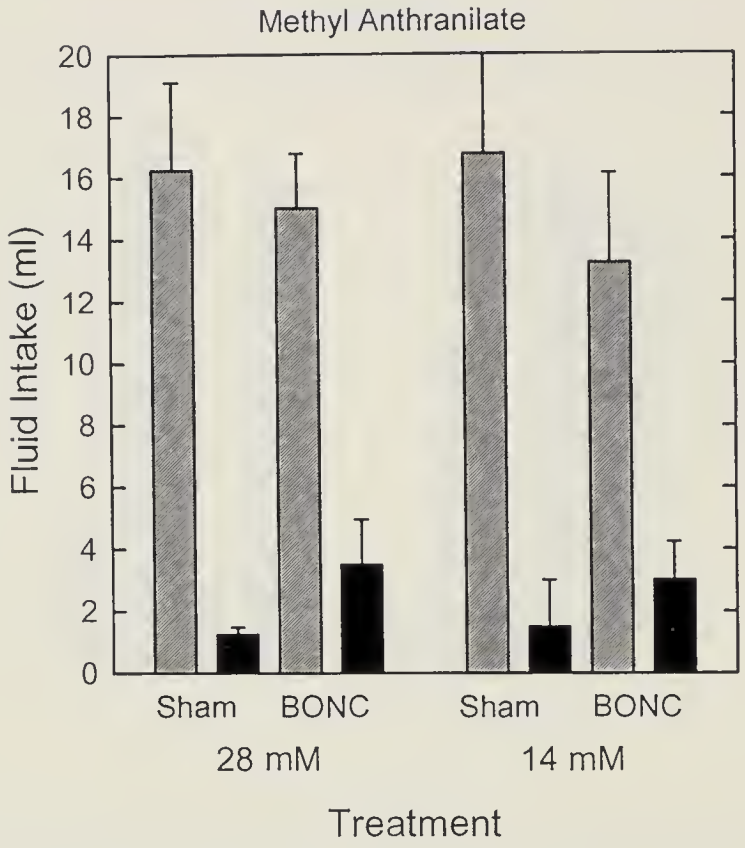

FIG. 7. Average fluid intake for MA as a function of a solution's molar concentration, surgery, and treatment period. Starlings were presented with tap water during the pretreatment period (hatched bars) and a MA solution during the treatment period (solid bars). Capped vertical bars depict one standard error.

oral contact with the substance (Experiment 2). Moreover, the prolonged exposure to repellents (OAP and MA) over several days failed to result in a learned odor avoidance (Experiment 3). These findings suggest that starlings do not readily learn to avoid solutions associated with the odor of repellents. The failure to form a conditioned avoidance is independent of the history of exposure to odors or repellent solutions (Experiment 2). Experiment 4 showed the lack of importance of olfactory cues in avoiding repellents. Surgical elimination of the olfactory nerves did not cause birds to increase consumption of repellent-bearing solution as was expected if olfaction was the mediating mechanism for avoidance.

The lack of odor avoidance and contribution of the olfactory system in the avoidance response is consistent with previous speculation that sensory repellents are mediated by the trigeminal system, although the role of taste cannot be ruled out on the basis of these experiments alone. However, there is other evidence consistent with involvement of the trigeminal nerve for perception of OAP and MA. Mason et al. (1989)

showed that bilateral section of the OBTN virtually eliminated the avoidance response of starlings to anthranilates. There is also electrophysiological evidence that the OBTN is highly responsive to OAP and MA (Clark, unpubl. data). Molecular modelling evidence suggests birds have a receptor mechanism that is responsive to anthranilates and acetophenones and is analogous to the vanalloid pain receptors in mammals (Clark and Shah 1994). Finally, even after central taste nuclei are ablated, chickens continue to avoid MA (Benowitz 1964), suggesting that taste is not critical in mediating the avoidance response.

The unsuitability of oral exposure to repellents as the unconditional stimulus may be attributable to its mode of action and/or localization. The trigeminal repellents tested appear to be unpalatable but do not cause illness (at least for the quantities voluntarily consumed by birds). In addition, the aversive effect is localized in the mouth (in this experiment) and not in the gastrointestinal system. Thus, repellents that are unpalatable and cause oral stimulation, in combination or alone, may be ineffective as unconditional stimuli relative to repellents that cause illness and gastrointestinal stimulation. This does not suggest that trigeminal repellents are poorer repellents than associative repellents. Both can be potent and result in strong avoidance behavior. The difference between the two repellent types is that birds fail to learn from their aversive experience with trigeminal repellents.

From a practical viewpoint, failure to learn about the sensory attributes of a repellent is not crippling to the objective of bird repellency. Laboratory and field studies show birds continuously sample small quantities of substances treated with sensory repellents (e.g., Mason et al. 1985, Clark and Shah 1991, 1994; Avery and Decker 1994). While total amounts consumed are small, how does the trigeminal repellent work to repel birds away from an area? The effectiveness of the repellent is twofold. In the first case, the repellent has a direct effect on individuals. When movement is not restricted, a bird encountering a sensory repellent quickly moves on to a more palatable resource patch (Mason et al. 1985). This observation is consistent with optimal foraging theory (Charnov 1976) and the proposition that low rates of energy return in a patch will favor the probability of abandoning that patch (Lima 1985). The repellent can be viewed as signalling low energy return or physically achieving the fact. Regardless, the outcome is the same. Second, as a consequence of reduced residency time in a patch, the recruitment opportunities to that patch are reduced. Thus, the number of birds that might visit the patch because they observe other individuals in the patch is reduced (Krebs 1974).

The inability to learn to stay away from sensory cues associated with

trigeminal repellents has implications for the evolution of plant-bird interactions as well. The behavior for free-ranging birds is to sample fruit throughout its development, apparently giving more attention to the salient chemical cues associated with palatability rather than ancillary sensory cues (Willson and Comet 1993). To prevent untimely frugivory, it is to the plant's advantage to employ transient protection to fruits and have birds return to the fruits at a later time when the seeds are ready for dispersal, rather than have birds form a strong conditioned avoidance response (e.g., Brower 1969, Guarino et al. 1974, Mason 1989). These observations provide intriguing interpretive possibilities about how chemical defenses of fruit should be structured to exploit the sensory systems and learning capabilities of birds. Chemical defenses in unripe bird dispersed fruit should consist of trigeminal repellents and not compounds that cause gastro-intestinal illness. Finally, a better understanding of how plants prevent untimely frugivory will prove invaluable in the design of nonlethal repellents for safe wildlife management strategies.

ACKNOWLEDGMENTS

I thank D. Coleman for assistance in the laboratory. C. A. Smeraski kindly performed the histological preparations. This study was supported by the United States Dept. of Agriculture cooperative agreement 12-34-41-0040 between the Monell Chemical Senses Center and the Denver Wildlife Research Center. All experimental procedures meet guidelines set forth by Monell's institutional animal care committee.

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Wilson Bull., 108(1), 1996, pp. 53–60

NEST-SITE SELECTION BY HOODED WARBLERS IN BOTTOMLAND HARDWOODS OF SOUTH CAROLINA

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BRIAN R. CHAPMAN, AND KARL V. MILLER

ABSTRACT.—We measured habitat features at 45 nests of Hooded Warblers (*Wilsonia citrina*) and 45 non-use sites in bottomland hardwood habitats in the coastal plain of South Carolina during the breeding seasons 1993–1994 to determine features that affect nesting success. Hooded Warblers nested in switchcane (*Arundinaria gigantea*) and hardwood saplings or shrubs that averaged 1.76 ± 0.10 m (*SE*) in height. Nests were more concealed from above ($P = 0.001$) and from the side ($P = 0.002$) than surrogate nests placed at non-use sites but were less concealed from below ($P = 0.002$). Nest sites also had a greater number of potential substrates ($P = 0.014$) in the nest patch (5-m radius) and greater measures of vegetation density ($P < 0.05$) in the nest patch than non-use sites. Successful nests differed from unsuccessful nests only in the amount of fern cover in the nest patch (greater for successful nests, $P = 0.012$). Fern cover may influence nesting success through an effect on behavioral defense strategies. Nesting success of Hooded Warblers may largely be unrelated to fine-scale differences in vegetative characteristics of the nest site. *Received 28 Mar. 1995, accepted 20 Sept. 1995.*

Because availability of suitable nest sites may be the most critical determinant of habitat selection (and thus perceived habitat quality) by some birds (Steele 1993), knowledge of what constitutes a suitable nest site, or more importantly a successful nest site, is necessary (Martin 1993a). For example, Martin and Roper (1988) found that successful Hermit Thrush (*Catharus guttatus*) nests were characterized by a greater density of white fir (*Abies concolor*) saplings in the 5-m radius circle surrounding the nest. Such specific habitat features that affect nest fate should be identified for other species.

Hooded Warblers (*Wilsonia citrina*) have been classified by the Partners In Flight prioritization scheme as a species of "very high concern" in the Southeast (Hunter et al. 1993a, b). We examined nest-site selection patterns of Hooded Warblers to determine habitat differences between successful and unsuccessful nests. We measured variables at two scales, the nest site and the nest patch. Hooded Warblers inhabit moist mature deciduous forests of eastern North America (Bent 1953, Powell and Rappole 1986, Evans Ogden and Stutchbury 1994). In the coastal plain of the southeastern United States, Hooded Warblers occur almost exclusively in forested wetlands (Bent 1953) and reach their greatest abundance in bottomland hardwood forests (Oak-Gum-Cypress [*Quercus-Nyssa-Taxodium*] association).

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STUDY AREA AND METHODS

We conducted this study at the U.S. Dept. of Energy's Savannah River Site (SRS), a 78,000-ha tract in Aiken, Barnwell, and Allendale counties, South Carolina. These counties lie in the Upper Coastal Plain physiographic province. Elevation ranges from <25 m at the Savannah River to 80 m at headwater streams (Workman and McLeod 1990). Bottomland hardwood forests are found along stream courses and may be seasonally flooded, usually during late winter–early spring. Dominant canopy species include sweetgum (*Liquidambar styraciflua*), swamp tupelo (*Nyssa sylvatica* var. *biflora*), red maple (*Acer rubrum*), water oak (*Quercus nigra*), and diamond-leaf oak (*Q. laurifolia*). Dominants in the mid-story include American holly, (*Ilex opaca*), sweet bay (*Magnolia virginiana*), red bay (*Persea borbonia*), and ironwood (*Carpinus carolina*). Switchcane (*Arundinaria gigantea*) and dog hobble (*Leucothoe axillaris*) dominate the shrub layer, and ferns, primarily netted chain fern (*Woodwardia areolata*) and Christmas fern (*Polystichum acrostichoides*), are the dominant ground cover (Workman and McLeod 1990). Bottomland study sites ranged in width from <50–>1000 m and were adjacent to closed-canopy pine (*Pinus elliottii* and *P. palustris*) forest.

We located Hooded Warbler nests in 11 bottomland hardwood strips during May–June 1993 and 1994 by observing adult behavior and by searching potential nesting habitat. We found most nests during the incubation stage. We were unable to determine whether nests were first or second attempts because individual birds were not marked and territories were not mapped. We monitored nests at 3–4 day intervals (Ralph et al. 1993) to determine nest fate. Nests containing nestlings on the last visit before the expected fledging date were assumed to have fledged. We defined successful nests as those that fledged at least one nestling. Vegetation measurements were made following termination of the nesting attempt. We made measurements at the nest plant and in the nest patch, defined as the 5-m radius circle centered on the nest plant (Martin and Roper 1988). Vegetation measurements then were repeated at an unused site. We located non-use sites by pacing 35 m (Ralph et al. 1993) upstream or downstream (determined by coin toss) in a direction parallel to the general bearing of the bottomland strip. This procedure located non-use sites outside of the nest patch but within the bottomland habitat. Non-use sites were centered on the plant stem nearest to the 35-m point that was of the same species and approximate size as the substrate plant (Ralph et al. 1993). Thus, equal numbers of nest sites and non-use sites were sampled. Success data were obtained from 36 nests, 15 nests in 1993 (8 successful, 7 unsuccessful) and from 21 nests in 1994 (10 successful, 11 unsuccessful). Eight additional nests in 1993 and one nest in 1994 that were empty when found were sampled and included in the comparison of nest sites versus non-use sites but not in the analyses relating to nest success (Martin and Roper 1988).

Measurements taken at the nest site included plant species used as the nesting substrate, nest height, plant height, and percentage of nest concealment. Concealment indices (0–4: 0 = 0% concealed, 1 = 1–25% concealed, 2 = 26–50% concealed, etc.) were estimated by viewing the nest from above and below and at nest level from a distance of 1 m in each of the four cardinal directions (Martin and Roper 1988, Holway 1991). For concealment estimates at non-use sites, an empty Hooded Warbler nest was placed at nest-height (i.e., the height of the nest corresponding to the non-use site) in the surrogate substrate plant (Holway 1991).

Measurements taken in the nest patch included overstory canopy cover, stem density of potential nest substrates and trees, fern cover, other herbaceous ground cover, and vegetation profile. Canopy cover above the patch was estimated by five hit-miss readings through an ocular tube (James and Shugart 1970), one at the nest plant and one in each of the cardinal

directions from the perimeter of the patch. Potential substrate and tree (woody stems > 3 m tall) densities were measured in five 1-m^2 quadrats located randomly along the four cardinal directions (transect and position on transect were randomized). Potential substrates were defined as switchcane >1 m tall and other woody species 1–3 m tall. Percent foliage cover of ferns and of other herbaceous ground cover also was estimated (0–4) within the quadrats. Vegetation profile of the patch, which may be viewed as an index of concealment at the scale of the patch, was determined using a 3-m tall vegetation profile board (Nudds 1977, Noon 1981) against which percentage cover was estimated (0–4) for each 0.5-m interval. The profile board was located at the nest plant and was read from a distance of 5 m in each of the cardinal directions.

For comparisons involving potential substrate density, nests were classified as either "switchcane" or "other", depending on the species of their actual substrate. Stem density of switchcane then was determined for switchcane nests and of other for other nests. Thus, the potential substrate variable was a nest-specific measurement which circumvented the problem, e.g., of comparing average switchcane density across all nests when only a portion of nests were in switchcane. Similarly, one vegetation profile measurement (nest level) was nest-specific. The profile readings for the 0.5-m interval corresponding to the height of each nest were compiled for the variable vegetation profile at nest level.

Univariate comparisons were made between Hooded Warbler nest sites and non-use sites and between successful and unsuccessful nest sites for each habitat variable. Variables estimated with the 0–4 index were compared with a Wilcoxon rank-sum test. All other comparisons were made with a two-sample *t*-test. Variances were assumed to be equal for comparisons in which the sample sizes were the same. When sample sizes differed, the *F*-test for equality of variance was used to test the equal variance assumption. Equal variance tests always were appropriate. Because no differences ($P > 0.05$) were found between years for any variables, data from both years were pooled.

RESULTS

Hooded Warblers selected saplings of nine different species as nest substrates: switchcane, 20 (44%); red bay, 7 (16%); common gallberry, 5 (11%); American holly, 5 (11%); water oak, 2 (4%); diamond leaf oak, 2 (4%); blueberry (*Vaccinium* spp.), 2 (4%); wax myrtle (*Myrica cerifera*), 1 (2%); and black oak (*Quercus velutina*), 1 (2%). Mean height of the nest plant was 1.76 ± 0.10 m (*SE*). With one exception, in which the nest was located in an upright branch of an American holly, nests were placed in crotches of the main stem and primary branches of the substrate plant. Nest height averaged 0.98 ± 0.36 m.

Hooded Warbler nest sites differed from non-use sites in several ways. Concealment of nests from above and from the side was greater ($P < 0.005$) at nest sites than at non-use sites, but from below was lower ($P = 0.002$) at nest sites than at non-use sites (Table 1). Potential substrate density was greater ($P = 0.014$) at nest sites (3.79 ± 3.37 stems/m^2) than at non-use sites (2.08 ± 1.88 stems/m^2). Vegetation profile measures for all heights and at nest level were greater ($P < 0.05$) at nests sites than at non-use sites (Table 1). Conversely, only one difference was determined

TABLE 1

COMPARISON OF MICROHABITAT VARIABLES ($\bar{x} \pm$ SE) AT HOODED WARBLER NEST SITES (N = 45) WITH THOSE AT RANDOM SITES (N = 45) WITHIN BOTTOMLAND HARDWOODS, SAVANNAH RIVER SITE, SOUTH CAROLINA 1994–1994

Parameter	Nest site	Random site	*P*
Nest site			
Nest height (m)	0.98 ± 0.05	1.01 ± 0.05	
Plant height (m)	1.76 ± 0.10	1.78 ± 0.14	
Concealment[a]			
Side	1.93 ± 0.10	1.50 ± 0.08	0.002
Above	3.36 ± 0.13	2.40 ± 0.21	0.001
Below	1.58 ± 0.16	2.09 ± 0.14	0.002
Nest patch			
Canopy cover[b]	4.36 ± 0.10	4.49 ± 0.10	0.360
Potential substrate density[c]	3.79 ± 0.60	2.08 ± 0.33	0.014
Fern cover[a]	1.19 ± 0.12	1.31 ± 0.16	0.842
Ground cover[a]	1.48 ± 0.10	1.69 ± 0.12	0.268
Vegetation profile[a]			
0.0–0.5 m	3.07 ± 0.10	2.68 ± 0.13	0.025
0.5–1.0 m	3.39 ± 0.10	2.83 ± 0.14	0.000
1.0–1.5 m	3.12 ± 0.09	2.36 ± 0.14	0.000
1.5–2.0 m	2.94 ± 0.13	2.14 ± 0.14	0.000
2.0–2.5 m	2.53 ± 0.14	2.02 ± 0.22	0.002
2.5–3.0 m	2.30 ± 0.14	1.79 ± 0.13	0.007
Mean	2.88 ± 0.08	2.31 ± 0.10	0.000
Nest level	3.47 ± 0.08	2.86 ± 0.11	0.000

[a] Index of percent coverage: 0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%. Index values were compared with the Wilcoxon rank-sum test; all other comparisons were made with a two-sample *t*-test.

[b] Estimated as the sum of five hit-miss readings taken within the patch (5 = total canopy closure).

[c] Stem density (# stems/m^2) of the plant species used as substrate. Substrates were categorized as switchcane or other (woody stems 1.0–3.0 m). Sample includes switchcane nests from 1993 and 1994 (N = 20) and other nests from 1994 (N = 12; total sample = 32).

for the comparison between successful and unsuccessful nests: fern cover was greater ($P = 0.012$) around successful nests.

DISCUSSION

Nest-site characteristics.—Switchcane best provides the structural features of a nest substrate sought by Hooded Warblers of all plant species occurring in bottomland hardwood habitats at SRS. It apparently is the preferred substrate species throughout much of the southeastern United States (Sprunt and Chamberlain 1949, Burleigh 1958). Switchcane is a woody grass (Poaceae) that may grow to 10 m (Radford et al. 1964) but normally ranges from 1–3 m. It commonly forms extensive thickets, or canebrakes, in southeastern swamps. In addition to the nests that were in

switchcane, many of the other nests were in saplings growing in canebrakes (i.e., switchcane provided most of the cover for most nests).

A variety of other plant species also were used as nest substrates. Hooded Warblers reportedly prefer mountain laurel (*Kalmia latifolia*), American holly, and fetterbush (*Lyonia* spp.) in other parts of their range (Bent 1953). All of these species are thicket-forming shrubs (during the sapling stage for American holly). Thus, Hooded Warblers may select shrubs, regardless of species, not only for their microsite characteristics but also for their thicket-forming properties, as evidenced by the greater density of potential substrates within the nest patch than at non-use sites. Holway (1991) found that species preference by another shrub-nesting warbler, the Black-throated Blue Warbler (*Dendroica caerulescens*), also was site-specific; they selected the understory shrub that offered the best protection from weather and predators.

Hooded Warblers selected nest sites that were less concealed from below than nests at non-use sites. Bent (1953, p. 613) quotes one author who said that "the easiest way to locate a [Hooded Warbler] nest was to place [his] head close to the ground, scan the low open spaces and look for a clump of leaves, which sooner or later proved to be a nest." The adaptive advantage of an opening immediately below the nest is unclear, though it may be related to escape strategies. Although Hooded Warblers normally do not approach or leave the nest near the ground (Odum 1931), when flushed, the female often drops from the nest straight to the ground before flying away just above the ground for a short distance (J. C. Kilgo, pers. obs.; Evans Ogden and Stutchbury 1994). Alternatively, such openings may result simply from the greater shading provided by the understory.

Murphy (1983) and Martin (1992, 1993a) have suggested that predation, because it is the primary cause of nest failure, should be the key factor influencing nest-site selection. Selection of nest sites with dense vegetation theoretically can inhibit predator efficiency by visually screening the nest and parent activity, by providing too many potential nest sites for the predator to search, and by physically impeding predators (Holway 1991). Our results indicate that Hooded Warblers may utilize each of these strategies in their selection of nest sites. Hooded Warblers selected nest sites that were better concealed from the side and from above than non-use sites. Furthermore, nest patches contained a greater density of potential substrates and denser vegetation profiles at all heights than non-use patches.

Effect of nest-site characteristics on success.—We detected no difference in concealment from any angle between successful and unsuccessful nests. Similarly, Howlett and Stutchberry (in press) detected no effect of

nest concealment on predation of Hooded Warbler nests in Pennsylvania, and Holway (1991) was unable to detect a relationship between concealment and the nest success of Black-throated Blue Warblers. We also failed to detect a difference in the number of potential substrates between successful and failed nests, as predicted by Martin and Roper (1988) and Martin (1993a). Several factors may make statistical distinction of these subtle habitat features difficult. First, Holway (1991) suggested that predators using olfactory cues would be less inhibited by visual concealment. Furthermore, nest predation sometimes can be random, with some nests being found by chance alone. Second, human visitation of nest sites during monitoring may have increased the likelihood of predation, and thus masked any effects of habitat on predation (Westmoreland and Best 1985, Martin 1992). Finally, all nests of shrub-nesting woodland birds should be concealed because selection of poorly concealed sites should be eliminated by natural selection (Wray and Whitmore 1979). The latter prediction is contradicted by several authors who have detected differences in concealment between successful and failed nests (e.g., Nolan 1978, Wray and Whitmore 1979, Martin and Roper 1988). However, Wray and Whitmore (1979), suggest that the apparently nonadaptive trait to select poorly concealed nest sites may be maintained in Vesper Sparrows (*Pooecetes gramineus*) because annual variation in their environment may permit the occupancy of a variety of nest sites to be adaptive over time. Although such temporal variation is probably great in the early successional habitats of Vesper Sparrows, the environments of mature forests are relatively stable. In addition, nest predation generally is higher in shrub and grassland habitats than in mature forests (Martin 1993b). Thus, a relationship between concealment and success should not be as evident in forested habitat. Studies of woodland shrub-nesting passerines support this contention (Best and Stauffer 1980, Conner et al. 1986, Holway 1991, Howlett and Stutchbury, in press; but see Martin and Roper 1988), whereas results of studies of birds in earlier successional habitats are more variable (Caccamise 1977, Best 1978, Nolan 1978, Wray and Whitmore 1979). Much of the predation on shrub-nesting woodland birds may largely be unrelated to fine-scale differences in concealment (Holway 1991).

The difference in fern cover between successful and failed nests is intriguing. This finding may be related to nest-defense strategies. Female Hooded Warblers almost invariably drop to the ground when flushed from the nest, and rather than flying away, they often engage in a distraction display, which consists of running through the underbrush with wings drooped and tail spread (J. C. Kilgo, pers. obs.; Evans Ogden and Stutchbury 1994). This behavior likely is their primary (if not only) means of nest defense. If insufficient ground cover exists in the patch to make this

technique effective (i.e., if the bird must itself escape and is not able to risk distracting the predator) the nest may be rendered more susceptible to predation. Ferns may provide structure that conceals the displaying female yet is sufficiently open to allow the predator to detect her. Thus, degree of fern cover may be one of the subtle habitat features that determines nest fate of Hooded Warblers. This may also explain why the more obvious measures of concealment and vegetation density did not differ between successful and failed nests.

ACKNOWLEDGMENTS

This study was funded by the United States Dept. of Energy, Savannah River Site, the United States Forest Service, Savannah River Forest Station Biodiversity Program, the Univ. of Georgia, and McIntire-Stennis Project No. GEO-0074-MS. J. Blake provided logistical support. We thank the many field assistants who helped in locating and monitoring nests and measuring vegetation. We thank G. W. Ware for providing statistical advice and A. S. Johnson, K. C. Parker, R. J. Warren, and D. H. White for reviewing the manuscript. L. B. Best and B. J. Stutchbury also provided valuable editorial comments.

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Wilson Bull., 108(1), 1996, pp. 61–71

CHANGE IN BODY MASS OF FEMALE COMMON GOLDENEYES DURING NESTING AND BROOD REARING

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ABSTRACT.—We measured body mass of female Common Goldeneyes (*Bucephala clangula*) during nesting on fish bearing lakes in northcentral Minnesota, in 1982–1985. Median body mass during egg laying was 775 g. Female mass during incubation varied among lakes and possibly years. Mass at the start of incubation (698–715 g) was 10.7–11.0% greater than that at hatching. Females regained most of the mass lost during incubation by the time they abandoned their class IIC or class III ducklings. Goldeneyes in Minnesota weighed less at the start of nesting than those studied on predominately fishless Ontario lakes; proportional mass loss during incubation was also substantially less than that reported in Ontario (approximately 20%). Differences in body mass dynamics may be related to the relative ease of food acquisition during nesting; foods might be acquired more easily in more productive wetlands despite the presence of fish. *Received 24 Feb. 1995, accepted 1 Sept. 1995.*

Relationships among incubation behavior, female body mass, and types of nutrients and energy sources used by temperate nesting waterfowl are understood reasonably well. In general, species that begin nesting earlier have greater body mass, forage relatively less while nesting, rely more on endogenous resources, and lose proportionately more mass during incubation than do later nesting species (see review in Afton and Paulus 1992). Common Goldeneyes (*Bucephala clangula*) deviate somewhat from this pattern. Although they are relatively small-bodied, females begin nesting soon after arrival when many wetlands are still ice-covered. Foraging territories also are defended vigorously during laying and early incubation (Savard 1984, Zicus and Hennes 1993). In addition, laying rates are low compared to other similar-sized waterfowl (cf Palmer 1976), and clutch mass can exceed female mass (Zicus, unpubl. data). These traits suggest that although females arrive with some stored reserves, exogenous nutrient sources may be important for clutch completion and female maintenance during incubation.

Mallory and Weatherhead (1993) recently predicted that female Common Goldeneyes lose approximately 18.5% of their body mass during incubation. Their prediction was based on relationships proposed by Afton and Paulus (1992) and appeared to be supported by data from an Ontario study where wetlands had been influenced extensively by acid

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deposition (Mallory et al. 1994). Harvey et al. (1989) concluded that Wood Duck (*Aix sponsa*) body mass dynamics during incubation varied substantially among and within individuals. They speculated that variability in Wood Duck incubation mass was related in part to fluctuating environmental conditions. Unfortunately, few published data relate local or regional environmental factors to body mass changes in other species of incubating waterfowl.

We describe body mass changes during nesting and brood rearing for female Common Goldeneyes in Minnesota. We examined the effects of different lakes and years and of changing reproductive stage on female body mass. Goldeneyes have been studied previously in areas where fish were absent or where goldeneyes appeared to favor fishless wetlands thereby avoiding dietary competition with fish during the reproductive period (Eriksson 1979, Eadie and Keast 1982, Blancher et al. 1992, and others). Whereas many lakes in Mallory and Weatherhead's 1993 study area were fishless (Mallory et al. 1994), each of our study lakes supported fish communities. Thus, our data should improve the understanding of goldeneye nesting biology where they commonly occupy fish-bearing lakes.

STUDY AREA AND METHODS

Female Common Goldeneyes were weighed during nesting on three lakes in Beltrami and Itasca counties of northcentral Minnesota. Refuge Pond, North Twin Lake, and Island Lake differed in size (46, 117, and 1250 ha, respectively), amount and type of public use, and use by goldeneyes (Zicus et al. 1995). The two larger lakes supported fish populations (dominated by Centrarchidae, Percidae and Esocidae) and were characterized by morphoedaphic indices (MEI) (Ryder 1965) of 6.75 and 18.01, respectively (Minn. Dept. Nat. Resour., Section of Fisheries, unpubl. data). These values are near optimum for highly productive fish communities (Ryder et al. 1974). The smallest lake supported only minnows. Females with hatched young were captured and weighed on Refuge Pond and Island and North Twin Lakes as well as on 10 additional lakes, each of which supported productive fish populations with species composition similar to those in the lakes where nesting ducks were weighed. These additional lakes had MEIs ranging from 4.52 to 21.78 (Minn. Dept. Nat. Resour., Section of Fisheries, unpubl. data).

Female Common Goldeneyes were captured before incubation began with nest traps (Zicus 1989) and again when we inspected nest boxes for use. Females were leg banded with U.S. Fish and Wildlife Service bands. Incubating female mass was measured when possible during weekly nest checks, and females accompanying broods were weighed when they were caught nest prospecting (Zicus and Hennes 1989) and during annual leg banding (Johnson 1972). Mass was determined to the nearest 5 g using spring scales and was unadjusted for female structural size.

Reproductive stage for egg-laying females was defined relative to the start of incubation, and that of incubating and brood-rearing females was referenced to the departure of young from nests. This differs from the convention often used for incubating females. However, we believe it is preferable because it allows corresponding days to be compared more appropriately. Reproductive stage of females with young from unmonitored nests was esti-

mated from the age of the majority of the ducklings in the brood. Duckling age was determined by comparison with known-age ducklings in various stages of plumage development. Plumage stages were assigned the following ages: IB—10 days, IC—18 days, IIA—27 days, IIB—35 days, and IIC—44 days.

We examined mass change of females before incubation using linear regression (PROC GLM; SAS Institute Inc. 1988). Year and location effects could not be examined because too few females were captured. Most females were weighed more than once during incubation, so we investigated their mass change using a generalized linear mixed model (GLMM) with maximum likelihood estimators (PROC MIXED; SAS Institute Inc. 1992). This approach allows measurements on subjects to be repeated within and across years. Dependencies among repeated measures are modelled explicitly and ensuing tests are adjusted for this dependence based on the underlying covariance structure (Laird and Ware 1982, Ware 1985). We determined (Jennrich and Schluchter 1986) that a compound symmetry covariance structure was optimal for our models. We modelled the effect of lake, year, linear, quadratic, and cubic effects of incubation day, and their interactions on female mass. When interactions were not significant ($\alpha = 0.05$), we used a reduced model. Log-likelihood ratio statistics were used to evaluate model goodness of fit, and simultaneous paired comparisons were made using a Bonferroni adjustment to pairwise differences in the time-adjusted means (Dobson 1990). Brood-rearing females were measured only once and their mass change was examined using linear regression (PROC GLM; SAS Institute Inc. 1988). We ignored possible lake and year effects because too few brood-rearing females were measured.

We further examined nonsignificant statistical results using post hoc power analyses (Anonymous 1995). Regression results were evaluated using a SAS MACRO (Latour 1992). Power calculations for the generalized linear mixed model were based on adjusted least squares effects estimated by PROC MIXED (SAS Institute Inc. 1992).

RESULTS

From 1982 to 1985, 45 females were weighed prior to or during egg-laying. In addition, 82 females were weighed repeatedly (1–5 times each year) for a total of 213 times at known points during incubation or with hatched young in the nest. One female was weighed in four years, five in three years, 25 in two years, and 51 in only one year for a total of 120 within-year time-series. During brood rearing, 63 females were weighed.

Prelaying and laying.—Reproductive status of females weighed before the start of incubation varied (Table 1). Those considered known nesters successfully incubated nests that we observed. Known nesters were weighed from one to 30 days before incubation (median = 15.5 days) and most likely represented females that were beginning to lay the clutch that they eventually incubated. In contrast, the sample of unknown status likely included females nesting elsewhere as well as those laying eggs parasitically when captured. We could not detect any linear trend in mass of known nesters during the laying period (mass change = 1.5 g/day, 95% confidence interval = −0.4 to 3.5).

Incubation.—We fit the GLMM to measurements of mass for females that successfully incubated a clutch. We detected no significant interac-

TABLE 1

MASS OF FEMALE COMMON GOLDENEYES CAPTURED DURING THE LAYING PERIOD IN NORTHCENTRAL MINNESOTA, 1982–85

Status	Mass (g)				N	Stage (days)[a]
	$\bar{x}$	SD	Median	Range		Median
Known nesters	768	34.0	775	685–810	16	15.5
Unknown	733	43.8	720	660–830	29	?

[a] Days prior to the start of incubation.

tions among the main effects (lake and year) and linear, quadratic, or cubic measures of incubation day (all Ps > 0.46) that affected mass loss. Two models, one linear and one cubic with incubation day, indicated mass was influenced by stage of incubation. The cubic model fit the data best ($G^2 = 16.48$, df = 2, $P < 0.001$) and indicated a curvilinear effect of stage on female mass (Table 2 and Fig. 1).

Body mass also was influenced by conditions related to specific lakes ($F = 2.72$; df = 2, 79; $P = 0.072$). Female body mass was greater throughout incubation on Island Lake than on North Twin Lake ($F = 4.29$; df = 1, 79; $P = 0.041$), but mass did not differ between Refuge Pond and either North Twin ($F = 0.00$; df = 1, 79; $P = 0.980$) or Island Lake ($F = 1.94$; df = 1, 79; $P = 0.167$) (Fig. 1).

We detected no effect due to different years with the GLMM ($F = 0.75$; df = 3, 125; $P = 0.523$), but graphical comparison of body mass of females for whom we had measurements in 1982 and 1983 suggested year might have an effect. Each of the four females was weighed at similar points during incubation both years, and each was 20–40 g lighter in 1983 than 1982 (Fig. 2).

Four of eight females that abandoned their nests during incubation had

TABLE 2

ESTIMATED COEFFICIENTS FOR POLYNOMIAL MEASURES OF INCUBATION DAY ON MASS CHANGE IN FEMALE COMMON GOLDENEYES FROM THREE NORTHCENTAL MINNESOTA LAKES, 1982–1985

Measure	$\hat{\beta}$	SE ($\hat{\beta}$)	P[a]
Day	6.3027	1.1799	<0.001
Day^2	−0.4127	0.0995	<0.001
Day^3	0.0083	0.0023	<0.001

[a] Two-sided test H_o: $\beta = 0$.

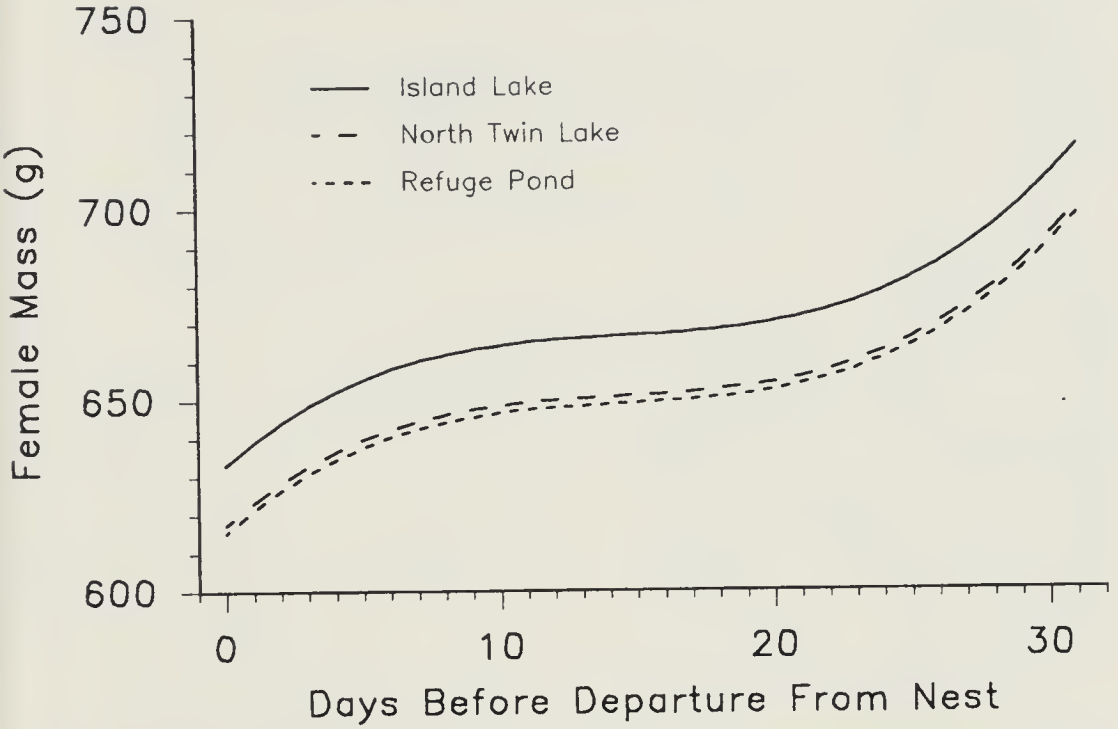

FIG. 1. Maximum likelihood estimates of cubic temporal trend in female Common Goldeneye body mass during incubation on three northcentral Minnesota lakes, 1982–1985.

a body mass greater than that predicted for successful females at the comparable point in incubation, and four were less than predicted.

Brood rearing.—Females in the composite sample regained body mass at approximately 2 grams/day ($F = 51.7$; df = 1, 62; $P < 0.001$) from the low they had reached when the young departed the nest (Fig. 3). Females apparently regained most of the body mass lost during incubation by the time they left their broods of class IIC or class III ducklings to molt.

DISCUSSION

Our results differed markedly from previous measurements of Common Goldeneye mass. Minnesota goldeneyes appear to weigh less at the onset of nesting than do Ontario birds. Mallory (1991:17) reported that prelaying females averaged 875 g at his Wanapitei study site and 842 g at a site farther east. These values are 67–100 g more than our median at the start of laying and 12–45 g more than our heaviest females. Whether females truly differ to this extent is unclear. Our sample of prelaying females was small, and we weighed females at various times during prelaying and laying. Furthermore, the Wanapitei values are estimates obtained by adjusting female mass determined during incubation to account

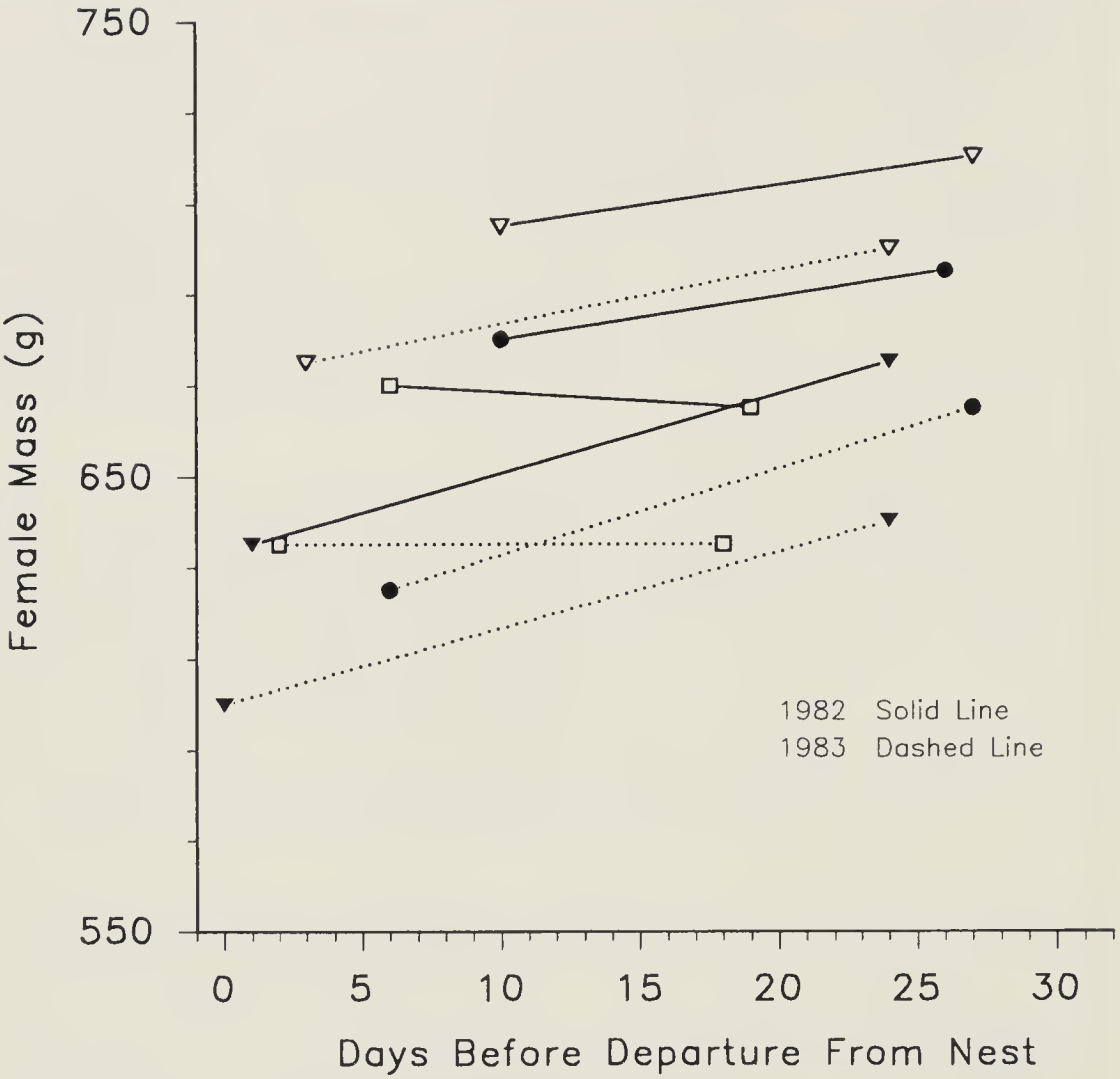

FIG. 2. Body mass of individual female Common Goldeneyes measured during incubation while nesting on three northcentral Minnesota lakes, 1982 and 1983. Individual females are identified by unique symbols.

for incubation mass loss and that assumed lost in the course of laying a clutch (Mallory 1991:16–17). Goldeneye females have been reported to lose approximately 22 g/egg (i.e., approximately 11 g/day) during egg laying (H. G. Lumsden, unpubl. data cited in Mallory 1991). We did not detect this sort of change in Minnesota, and there was sufficient power (>0.99) to detect a change of as little as 6 g/day. Projected mass of Wanapitei females may be biased high because mass loss per egg in Ontario is now believed to be <22 g (M. L. Mallory, Environ. Can., pers. comm.). Nonetheless, model predictions of mass for Minnesota females at the start of incubation ranged from 698–715 g depending on factors associated with the nesting lake. In contrast, Ontario goldeneyes appear

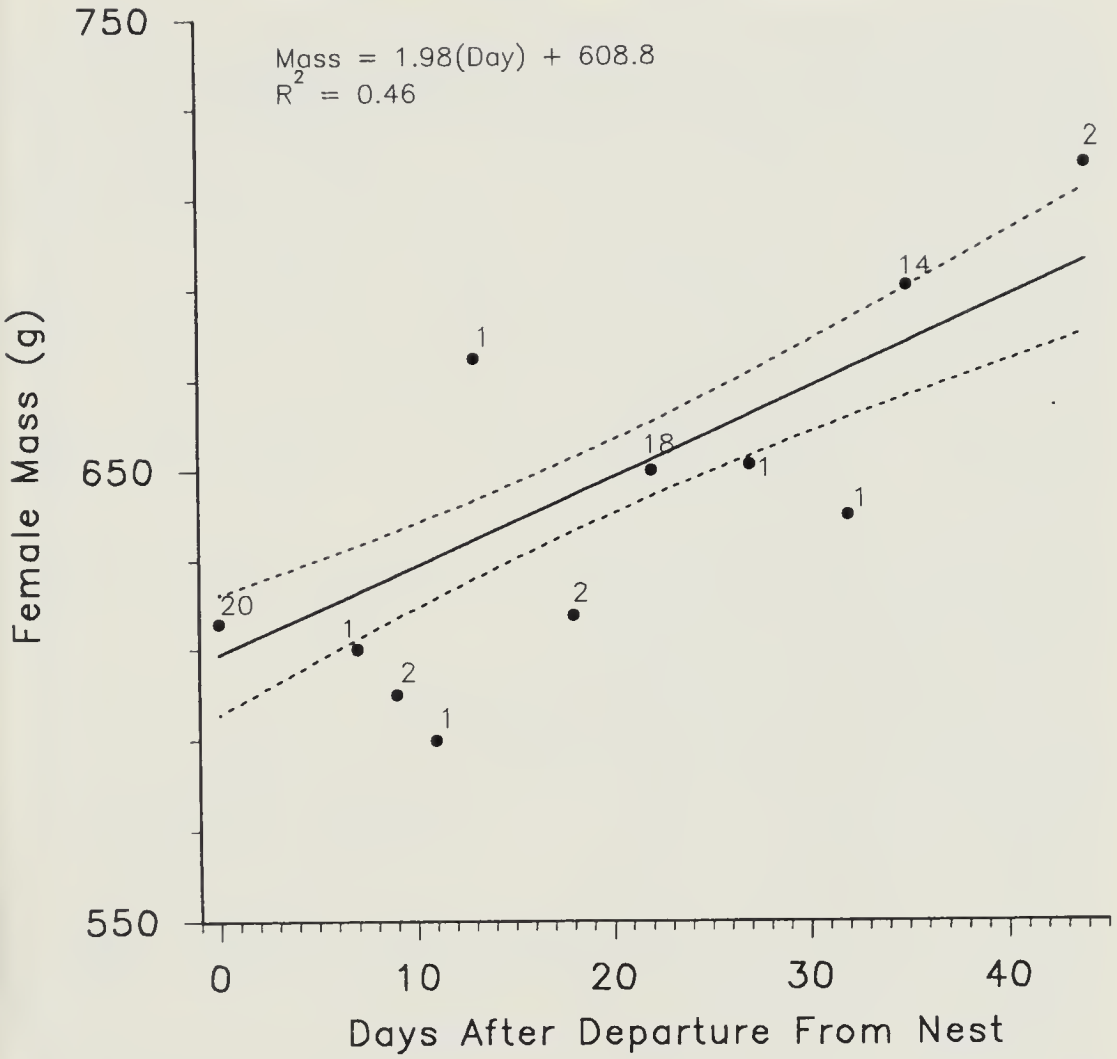

FIG. 3. Linear regression predictions (±95% confidence limits) and observed mean body mass (sample sizes) for female Common Goldeneyes with hatched young on 12 northcentral Minnesota lakes, 1982–1985.

to begin incubation at 752–829 g (calculated from Mallory and Weatherhead 1993).

Minnesota goldeneye females lost proportionately less mass during incubation than Ontario birds. Rate of mass change did not differ among nesting lakes or years, although our analysis indicated location and possibly year affected overall incubation mass. The proportionate mass loss by goldeneyes from the start of incubation until broods departed the nest (31 days) was 10.7–11.0% depending on the nesting lake. In comparison, Mallory and Weatherhead (1993) estimated mean mass loss variously and reported changes for Ontario goldeneyes of 16.7% (page 853), 17.8% (page 856), and 24.5% (calculated from equation page 853 using 31 days of incubation).

Incubating Common Goldeneyes apparently lose body mass in a nonlinear fashion (Mallory and Weatherhead 1993, this study). However, our analysis suggested a different pattern than that described for birds in Ontario. Minnesota goldeneyes experienced a rapid initial decline during early incubation, reduced rate of loss in mid-incubation, and an increased rate of loss again prior to hatching and duckling departure. Mass loss during incubation for Ontario females has been modelled as decreasing monotonically with the lowest mass occurring on the last day of incubation (Mallory and Weatherhead 1993:equation p. 853). However, Mallory and Weatherhead (1993:853) also indicated that some females reached their lowest mass as early as day 18 of incubation, after which some mass was regained.

Female mass when broods departed the nest was similar in Ontario and Minnesota, but again measurements are not directly comparable. Mallory and Weatherhead (1993:856) reported that mean body mass of 10 females at the end of incubation was 626 g. However, two of the females included in their sample had deserted their nests after 18 and 24 days of incubation, respectively. By comparison, Minnesota females were predicted to weigh 615–633 g on the departure day (model intercepts) depending on the lake. Unadjusted arithmetic mean mass on the day broods departed the nest was 616 g (N = 20).

Mallory and Weatherhead (1993) speculated that female goldeneyes that lost too large a proportion of their initial incubation weight or dropped below approximately 600 g might be more prone to nest abandonment than others. We observed no indication that mass of females deserting their nests differed from that of successful females, but more data are needed. Furthermore, seven of 20 successful females weighed the day ducklings departed the nest were less than 600 g and five were ≤580 g. Some females remained below 600 g well into brood rearing.

Methodology alone does not explain the marked differences in incubation mass and proportional mass change during incubation in our study versus those reported for Ontario goldeneyes. At least two explanations are tenable. In addition to the well known difference existing in geese, body size has been shown to vary geographically in some passerines (Aldrich and James 1991, Twedt et al. 1994). Ontario females may be structurally larger than those nesting in Minnesota and thus able to return to breeding areas with more stored reserves. Alternatively, Ontario females may be similar in size but may return with proportionately more stored resources (i.e., better condition). Several studies (e.g., Gatti 1983, Harvey et al. 1989, Aldrich and Raveling 1983) have reported that heavier individuals lost a greater proportion of their body mass in incubation than lighter conspecifics. Gatti (1983) reasoned that heavier Mallards (*Anas*

platyrhynchos) could afford to lose more mass than those in poorer condition. In contrast, Kennamer and Hepp (1987) reported that double-brooded Wood Duck females lost a smaller proportion of their body mass after their first nesting than single-brooded females and may have been in better condition as a result.

Whether Ontario females are structurally larger than those in Minnesota or just begin incubation in better condition, incubation constancy was similar in the two locations (Mallory and Weatherhead 1993, Zicus et al. 1995). Together with the disparate mass loss and comparable weights at the end of incubation, these results indicate that either differences in foraging time during incubation recesses exist or else Ontario females consume less food or food of lower quality during incubation than do Minnesota females. Most resident nesting goldeneyes from Island Lake and Refuge Pond appeared to forage exclusively on their respective lakes, whereas most females nesting on North Twin Lake foraged elsewhere. Zicus and Hennes (1993) observed nesting female goldeneyes feeding at least as much as most small-bodied waterfowl which rely extensively on exogenous resources. They also reported that time devoted to foraging during nesting varied among years and concluded that females foraged less when food was most available. Harvey et al. (1989) likewise believed that reduced food availability in some years contributed to a greater relative mass loss during incubation in Wood Ducks. Furthermore, incubation mass was lowest on Refuge Pond, the location among our three study sites where Zicus et al. (1995) reported low incubation constancy in a concurrent study. They speculated that low constancy was a consequence of increased foraging time because of more difficult food acquisition.

Goldeneye mass during incubation varied among the lakes that we studied. Although we detected no differences among years with the GLMM, measurement of a small sample of the same females in two consecutive years suggested that yearly differences of at least 20 g might exist in some years. The GLMM analysis had low power (0.46) at $\alpha = 0.05$ to detect such a difference. Nonetheless, the among lake and year mass differences we measured were less than differences between Minnesota and Ontario. Mann and Sedinger (1993) suggested that Northern Pintail (*Anas acuta*) females nesting in Alaska relied more on endogenous resources than temperate nesting congeners because of less productive high latitude wetlands. Goldeneyes might use different nesting strategies depending on average environmental conditions and food availability in the regions they occupy. In some regions, wetland productivity may be sufficient to provide adequate goldeneye food availability even in the presence of fish (DesGranges and Gagnon 1994:220). Resource acquisition would then be less constrained by female foraging time because food

could be acquired easily. Patterns of body mass change before and during incubation indicate this situation is likely in Minnesota. Alternatively, females might rely more on resources acquired before arrival to nesting areas where wetland productivity is low. If nesting strategy within the species is flexible, relationships among habitat quality, female mass, and reproductive effort and success (Mallory et al. 1994) may need to be reexamined.

ACKNOWLEDGMENTS

We thank N. L. Weiland, biologist on the Chippewa National Forest Blackduck District, and private landowners on North Twin and Island Lakes for permission to work with their waterfowl nest boxes. Numerous summer technicians with the Minnesota Department of Natural Resources helped capture and weigh brood females during routine leg banding. Discussions with and comments by M. A. Hanson, S. J. Maxson, R. T. Eberhardt, and D. P. Rave improved the manuscript. M. L. Mallory also reviewed an earlier draft of the manuscript.

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Wilson Bull., 108(1), 1996, pp. 72–79

INTERSPECIFIC VARIATION IN THE CALLS OF *SPHENISCUS* PENGUINS

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ABSTRACT.—We compared the vocal repertoires of Jackass (*Spheniscus demersus*), Humboldt (*S. humboldti*), and Magellanic (*S. magellanicus*) penguins. Discriminant and cluster analyses of the bray call indicate that Jackass and Magellanic penguins are more similar to each other than either is to the Humboldt penguin, and all three are distinct from the Rockhopper penguin (*Eudyptes chrysocome*). The congruence of the vocal analyses with phylogenies based on allozyme data suggests that differences in vocalizations reflect gradual divergence over time, not character displacement. *Received 1 Jan. 1995, accepted 20 Sept. 1995.*

Vocalizations frequently are used to assess taxonomic relationships in birds and the use of song in avian systematics has been thoroughly reviewed by Payne (1986). Vocalizations also have been used to determine phylogenies of non-passerine species such as the caledrine sandpipers (Miller et al. 1988). Jouventin (1982) found calls to be the best behavioral criterion for classifying penguins. The degree of variation in calls was used to infer subspecies and species status in island populations of nine penguin taxa. Vocalizations have been shown to be of primary importance in the communication of many penguin species (Pettingill 1960, Stonehouse 1960, Boersma 1974, Spurr 1975, Jouventin 1982). Although behavior has been studied in all of the *Spheniscus* penguins, only preliminary information exists concerning their vocalizations (Boersma 1974, 1976, Eggleton and Siegfried 1979, Jouventin 1982, Scolaro 1987).

Species status and phylogenetic relationships in the genus *Spheniscus* are not clearly defined. There is insufficient detail in the fossil record to distinguish among species (Simpson 1976). Morphological studies led Clancey (1966) to classify Jackass penguins (*S. demersus*) as a subspecies of Magellanic penguins (*S. magellanicus*). O'Hare (1989) used 22 morphological characters to clearly differentiate *Spheniscus* from other penguin genera. However, he was unable to determine the taxonomic relationships among species within the genus. Utilizing data from DNA-DNA hybridization, Sibley and Monroe (1990) proposed that *S. demersus* be viewed as a superspecies containing *demersus, magellanicus,* and the Humboldt penguin (*S. humboldti*). Recent allozyme analyses suggest that

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Humboldt penguins form a distinct species, but that Jackass and Magellanic penguins are closely related (Grant et al. 1994, Thumser and Karron 1994).

We quantitatively analyzed the vocalizations of three *Spheniscus* species (Jackass, Humboldt, and Magellanic penguins) and one outgroup (Rockhopper penguins, *Eudyptes chrysocome*). Their vocal repertoires were compared to determine if species consistently differ in the acoustical structure of their calls. A resulting phylogeny was compared to an independent phylogeny based on protein polymorphisms (Thumser and Karron 1994).

METHODS

Vocalizations of 21 Humboldt penguins were recorded at the Milwaukee County Zoo in Wisconsin (February 1986–May 1987, February–March 1988), the Brookfield Zoo in Chicago, Illinois (November 1987–April 1988), and the St. Louis Zoo in Missouri (October 1988). Recordings of 12 Jackass penguins were made at the Henry Villas Zoo in Madison, Wisconsin (January–April 1988), the Knoxville Zoo in Tennessee (May 1989), and the Racine Zoo in Wisconsin (February–March 1990). Seven Magellanic penguins were recorded at the Cincinnati Zoo in Ohio (April 1988) and by Jim Klinesteker at the John Ball Zoological Gardens in Grand Rapids, Michigan (Spring 1989). Eleven Rockhopper penguins were recorded at the Cincinnati Zoo (April 1988) and the St. Louis Zoo (October 1988).

This study was performed exclusively on captive penguins. Although the majority of recorded Jackass penguins were born in captivity, most of the Magellanic, Rockhopper, and Humboldt penguins were born in the wild. The birds comprising these captive populations may have been drawn from a limited number of wild populations. However, the results from this study should be representative since seabirds usually have limited variation in their vocalizations, particularly at or below the species level (Pierotti 1987).

Observations were made during breeding periods, mainly prior to and just after egg laying, since most of the calls occurred at those times. A microphone was placed inside the exhibit, but observations were made from outside the exhibit to minimize disturbance of the birds. Individuals were identified by tag color. General behavior was observed throughout the day (from 08:00 to 17:00 h CST). Notes were recorded on videotape (Hitachi HJ 5000) and by hand. Vocalizations were recorded throughout the period on a cassette recorder (Aiwa HSJ 500) using a Nakamichi (CM 100) microphone. Whenever possible the identity of the caller was noted. Peak periods of vocalization were simultaneously videotaped and tape-recorded.

The recorded calls were analyzed at 150 Hz bandwidth using a Kay 7800 Digital SonaGraph and digitized using a Sigma Scan (1988) Program. For the bray call, the number of syllables per call, total duration of the call, sum of the inter-syllable intervals, duration of the longest syllable, and minimum, main, and maximum frequency of the longest syllable were recorded. The main frequency represented the darkest band in the sonagram of the call. These seven variables were selected to assess the acoustic structure of the bray call based on both frequency and temporal components. In addition, these parameters were selected because they could be measured precisely.

The vocalizations were analyzed using discriminant and cluster analysis in SYSTAT (Wilkinson 1990). The bray call was selected for analysis since nested ANOVA of individuals within populations within species indicated significant differences at the species level for more than one parameter (Thumser 1993). The data set included all recorded bray calls of the three *Spheniscus* penguins and the Rockhopper penguins. There were 109 calls from

TABLE 1

DISCRIMINANT FUNCTION 1 SHOWING THE CORRELATIONS BETWEEN CONDITIONAL DEPENDENT VARIABLES AND DEPENDENT CANONICAL FACTORS IN FOUR PENGUIN SPECIES

Variable	Factor		
	1	2	3
Number of syllables	−0.289	−0.710	−0.024
Total duration	0.337	−0.652	0.401
Inter-syllable interval	0.270	0.018	−0.345
Duration of longest syllable	0.622	−0.229	0.559
Maximum frequency	0.008	−0.635	−0.075
Minimum frequency	−0.145	0.464	0.083
Main frequency	−0.292	0.257	0.544
Chi-square	496.75	213.17	39.61
df	21	12	5
P	<0.001	<0.001	<0.001
Correlation	0.764	0.644	0.339

Humboldt, 77 calls from Jackass, 38 calls from Magellanic, and 106 calls from Rockhopper penguins. Each of the bray call variables was standardized by converting its values to *z*-scores prior to analysis. In discriminate analysis known groups were used to generate linear models which gave the best fit for that grouping. The data were also analyzed to determine how well the model predicts the actual groupings. Another multivariate technique, cluster analysis, was used to detect natural groupings in data with no prior expectations. In this case, Pearson's distance measures and the single-linkage method were performed by calculating the mean of each of the standardized variables for each species.

RESULTS

For the first discriminant function, Factor 1 arranged the four species primarily on the basis of the duration of longest syllable and the total duration of the call, while Factor 2 was primarily based on the number of syllables, the total duration of the call, and the maximum frequency of the longest syllable (Table 1). Overall, the analysis correctly categorized 86% of Humboldt, 82% of Jackass, 52% of Magellanic, and 79% of Rockhopper penguin calls. These vocal parameters clearly separated the *Spheniscus* penguins from the outgroup, Rockhopper penguins (Fig. 1A). Therefore, the outgroup was removed from the analysis and a second discriminant analysis was run to increase the spread among the *Spheniscus* penguins. In this discriminant function, Factor A arranged the three species primarily on the basis of syllable number and maximum frequency of the longest syllable, and Factor B was based primarily on the duration and main frequency of the longest syllable (Table 2). The analysis correctly predicted 91% of Humboldt, 71% of Jackass, and 61% of Magellanic penguin calls. Within the *Spheniscus* penguins, there was consid-

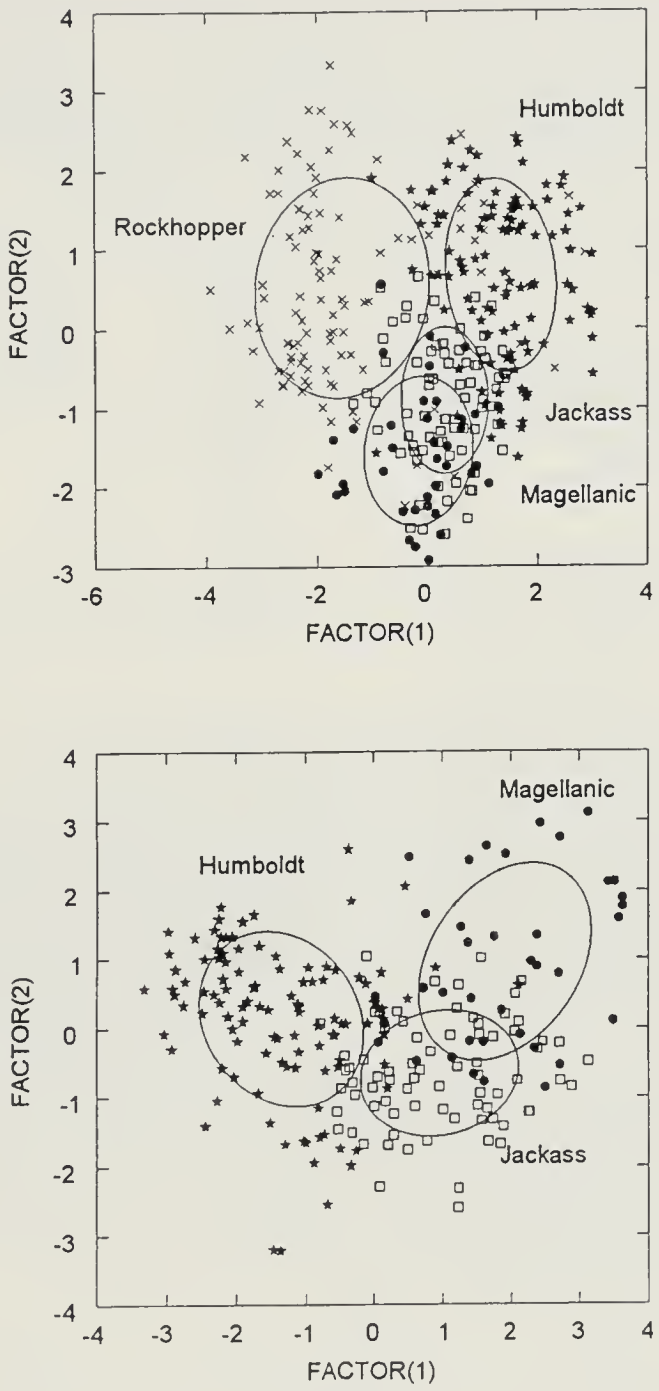

FIG. 1. (A) A scatterplot of the similarity between the bray calls of three *Speniscus* species (Jackass, Magellanic, and Humboldt) and an outgroup (Rockhopper penguins). (B) A scatterplot of the similarity between the bray calls of the three *Spheniscus* species. Both scatterplots have ellipses around 50% of the data points for Humboldt (dark star), Jackass (open square), Magellanic (dark circle), and Rockhopper (cross) penguins.

TABLE 2

DISCRIMINANT FUNCTION 2 SHOWING THE CORRELATIONS BETWEEN CONDITIONAL DEPENDENT VARIABLES AND DEPENDENT CANONICAL FACTORS IN THREE *SPHENISCUS* SPECIES

Variable	Factor	
	A	B
Number of syllables	0.711	−0.020
Total duration	0.311	0.319
Inter-syllable interval	−0.136	−0.274
Duration of longest syllable	−0.225	0.735
Maximum frequency	0.441	−0.065
Minimum frequency	−0.257	0.074
Main frequency	−0.041	0.423
Chi-square	287.22	60.23
df	14	6
P	<0.001	<0.001
Correlation	0.804	0.491

erable overlap in the vocalizations of Magellanic and Jackass penguins (Fig. 1B). In fact, 37% of the Magellanic penguin calls were incorrectly classified as Jackass penguin calls, and 12% of Jackass penguin calls were incorrectly classified as Magellanic penguin calls. By contrast, there was less similarity in the bray call parameters of Humboldt and Jackass penguins (Fig. 1B). Only 6% of the Humboldt penguin calls were incorrectly classified as Jackass penguin calls and 17% of the Jackass penguin calls were incorrectly classified as Humboldt penguin calls. Humboldt and Magellanic penguins were the least similar in their calls (Fig. 1B). In both species 3% of their calls were incorrectly classified as the other species. These results were supported by the cluster analysis shown in Table 3 and Figure 2. The distance matrix and tree show the Magellanic and Jackass penguins clustering closely together, the Humboldt penguins more distant, and the Rockhopper penguins the most distant.

TABLE 3

PEARSON'S DISTANCE MATRIX SHOWING THE DISTANCE BETWEEN FOUR PENGUIN SPECIES BASED ON SEVEN VARIABLES OF THE BRAY CALL

Species	1	2	3
1 Humboldt Penguin			
2 Jackass Penguin	1.304		
3 Magellanic Penguin	1.436	0.260	
4 Rockhopper Penguin	1.462	1.664	1.509

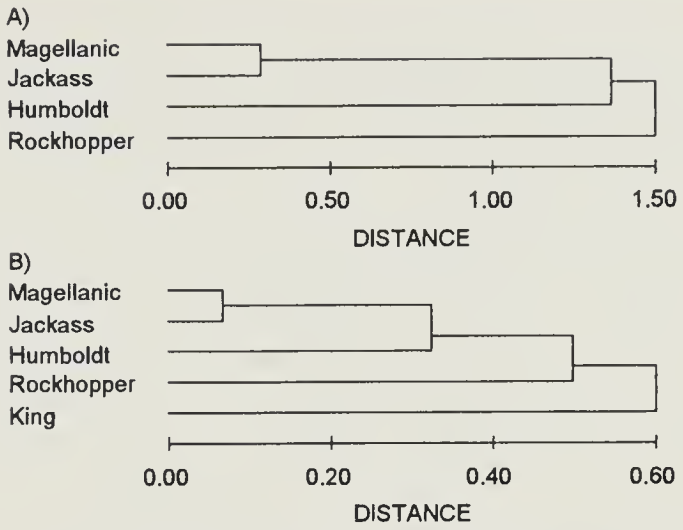

FIG. 2. (A) A tree using the single-linkage method based on Pearson's distances of parameters of the bray call. (B) UPGMA tree based on modified Rogers distance of allozyme data (Thumser and Karron 1994).

DISCUSSION

Overall, the *Spheniscus* penguins have retained a complement of calls that are similar in structure and function (Thumser 1993). The bray call is used to establish a territory and to advertise availability for pairing. The bird stands with its head pointing up and calls while slowly flapping its wings. This was the only call which showed sufficient species-level variation for phenetic analysis.

The analyses of selected vocal parameters of the bray call clearly distinguish Humboldt from both Jackass and Magellanic penguins. However, discriminant and cluster analyses often could not distinguish between the Magellanic and Jackass penguin calls. This may reflect the evolutionary relationships among the species or may have resulted from other factors. Since Humboldt and Magellanic penguins occur sympatrically in South America, another possible explanation for the differences in their breeding calls is character displacement. By contrast, the similarity of South American Magellanic and African Jackass penguin calls is unlikely to result from convergence.

In order to determine whether character displacement has occurred it is necessary to know which vocal characters are ancestral. It is difficult to root a tree based on vocalizations and determine the most ancestral species because vocalizations can be subject to strong selection. However, a comparison of allozyme variation enhances these results because protein markers are subject to weaker and different selective forces than those

influencing behavioral traits. Trees based on allelic characters are also more easily rooted using outgroup taxa.

The allozyme data were consistent in two different studies (Grant et al. 1994, Thumser and Karron 1994). Grant et al. (1994) based their analysis on 15 polymorphic loci in 75 captive (Humboldt, Magellanic) and wild (Jackass, Rockhopper, and Macaroni [*Eudyptes chrysolophus*]) penguins. Thumser and Karron (1994) studied nine polymorphic loci in 165 captive (Jackass, Humboldt, Rockhopper, King [*Aptenodytes patagonicus*]) and wild (Humboldt, Magellanic) penguins. In both studies, Jackass and Magellanic penguins were very closely related and Humboldt penguins clearly formed a distinct species. There is a striking similarity of phenetic trees based on the allozyme data and the vocal analysis presented here (Fig. 2). Cladistic analysis of the allozyme data confirmed that *Spheniscus* penguins form a monophyletic group (Grant et al. 1994, Thumser and Karron 1994). These findings suggest that differences in vocalizations between the Humboldt and Magellanic penguins are not due to character displacement, but rather reflect gradual genetic divergence of separate evolutionary lineages. Although the Humboldt and Magellanic penguins occur sympatrically, they have lower genetic identities and greater vocal differences than the more closely related Jackass and Magellanic penguins.

ACKNOWLEDGMENTS

This research was partially funded by grants from the Ruth Walker Scholarship Fund, the Univ. of Wisconsin–Milwaukee Graduate School, and the Institute of Museum Services (IC-10197-91). We thank the following zoos for allowing access and providing assistance in recording penguin vocalizations: Brookfield, Cincinnati, Henry Villas Park, Knoxville, Milwaukee County, Racine, and St. Louis. We are also grateful to Jim Klinesteker at the John Ball Zoo for providing us with recordings of a Magellanic penguin population. P. D. Boersma, G. Miller, and an anonymous reviewer provided several helpful suggestions on an earlier version of the manuscript.

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Wilson Bull., 108(1), 1996, pp. 80–93

THE BREEDING BIOLOGY OF THE WILLOW TIT IN NORTHEASTERN SIBERIA

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Abstract.—We studied the breeding biology of the Willow Tit (*Parus montanus*) during 1987–1990 in the Magadan region of northeastern Siberia. Clutch size and number of fledglings averaged 7.5 and 6.5, respectively, and both were correlated negatively with the date of the first egg. Nestling growth rate was correlated positively with the date of the first egg, but was not related to brood size. Body mass at fledging was related negatively to brood size. Males fed nestlings significantly more often than did females, while females spent more time attending nestlings. The number of parental visits per young did not change significantly with brood size. During the first 13 days of the nestling period, female feeding rate per young was positively related to brood size while for males this relationship was negative. The nestling diet consisted mostly of Lepidoptera larvae, Arachnoidea, and Diptera. *Received 20 April, 1995, accepted 21 Sept. 1995.*

Most studies of the Willow Tit (*Parus montanus*), a small hole-nesting Palearctic passerine, have focused on the species' non-breeding biology in northern Europe (see Ekman 1989, Matthysen 1990). Fewer studies have been done on its breeding biology (Orell 1983, Orell and Ojanen 1983, Pravosudov 1987, Orell and Koivula 1988, see review by Cramp and Perrins 1993). Here, we report details of breeding biology of the Willow tit in northeastern Siberia and compare it with breeding biology of other parids. Our study area is close to the easternmost part of this species' range.

METHODS

We collected data between 1987 and 1990 in the southern part of the Magadan region of northeastern Siberia (60°N, 150°E). The habitat was comprised mainly of larch (*Larix cajandery*), poplar (*Populus suoveolens*), and chosenia (*Chosenia arbutifolia*). A detailed description of the study area has been published previously (Pravosudov 1993a, b). Most of the birds were fitted with unique combinations of color bands. Nests were opened with a knife, after which a patch of bark was used to cover the opening. Nestlings in 13 nests were weighed to the nearest 0.1 g and the fifth primary was measured to the nearest millimeter. Using nonlinear regression, we found that the logistic equation was the most suitable for describing rate of body mass increase, and we used the growth constant K to estimate nestling growth rate. As another index of nestling growth, we used the growth of the fifth primary. The rate of increase in length of this feather is very close to linear, so we used the slope of the linear regression as an estimate of the growth rate. The rates at which nestlings were fed were studied by repeatedly observing eight nests for 1-h intervals over the whole nestling period. All observations were made from 35–40 m, and the parents did not appear

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to be disturbed by our presence. To collect food brought to each nestling by its parents, we used a thread tied loosely around each nestling's neck. After the parents made a number of feeding visits corresponding to the number of young in a nest, we collected the food loads from each nestling's throat with forceps and stored each load in a separate vial. Parents resumed feeding as soon as collared nestlings were put back in the nest. This method did not appear to harm the young tits. In 1987, we determined only the frequency of different prey items in the diet. In 1989 and 1990, we also weighed to the nearest mg each food load taken from a nestling and each individual item such loads contained. Over all years, we collected 296 food items contained in 108 individual loads from 11 broods, 185 of which were weighed. The number of food loads collected per nest was 5–23 loads. The food loads were collected from nestlings 6–12 days old, with most collected during 7–11 days of nestling age.

Multi-way general linear models (GLM) and multiple and simple linear regression analyses were used for the majority of tests. General linear model (GLM) is a multivariate analysis that is used to perform analysis of variances (ANOVA) with balanced and unbalanced designs, analysis of covariance (ANCOVA), and regression (Neter et al. 1990, Anonymous 1991). All analyses were performed using MINITAB routines (Anonymous 1991). All tests of the slopes in regression analyses and for covariates in the GLMs were two-tailed. For statistical analyses of parental feeding rates, we used two methods (1) we analyzed averages per nest for the whole nestling period (16 days), and (2) we used all observations (147 1-h periods) made repetitively at the eight nests in a GLM where each nest served as a factor. All models dealing with parental feeding rate consisted of a nest as a factor and nestling age and brood size as covariates. Analyses of the length of time that parents spent in the nest during one visit while feeding nestlings was done on three nests only, and all 579 such observations were used in a GLM where each nest served as a factor and brood size and nestling age served as covariates. For statistical analyses of variance in food loads and main prey type in the diet among different years and different broods, we used average frequency of every prey type in a load per nest in ANOVA. Thus, the brood was the primary sampling unit. To analyze variation in the diet among different broods, we used average frequency of every prey type in a load and the load was the primary sampling unit. The variation among broods was tested separately for each year.

RESULTS

Willow Tits almost always excavated their own cavities. Only two of 22 nests were in pre-existing natural holes, and in both cases, the birds altered the original hole by shaping the cavity. The average start of egg-laying differed significantly among years, occurring a week later during 1990 than during the two preceding years (ANOVA, $F_{2,18} = 5.7$, $P = 0.012$; Table 1). Mean clutch size was 7.5 eggs and varied significantly among years. Birds that started laying eggs later had smaller clutches (ANCOVA, effect of year, $F_{1,17} = 10.1$, $P = 0.006$; date of the first egg, slope $= -0.15$, $P = 0.006$; Table 1). The number of young that fledged was 6.5 and did not vary significantly among years, but pairs that started laying eggs later had significantly fewer fledglings (ANCOVA, effect of year, $F_{1,16} = 2.4$, $P = 0.124$; date of the first egg, slope $= -0.19$, $P = 0.03$; Table 1). Reproductive success as fledglings per egg averaged 0.85 and was nearly always higher than 0.7 (Table 1). The nestling body mass

TABLE 1

BREEDING CHARACTERISTICS OF WILLOW TITS IN THE MAGADAN REGION OF SIBERIA[a]

Parameter	1987	1989	1990	Total	Range
No. of nests	9	6	7	22	
Mean date of first egg	30 May	30 May	6 June	1 June	25 May–7 June
	1.6 days	1.9 days	1.7 days	5.6 days	
Clutch size	7.1	8.0	7.7	7.5	6–10
	0.4	0.5	0.4	1.1	
No. of fledglings	6.4	6.2	6.8	6.5	3–9
	0.6	0.7	0.7	1.6	
Reproductive success[b]	0.89	0.75	0.89	0.85	0.42–1.00
	5.2	6.1	6.1	15.5	
K constant	0.376	0.372	0.411	0.385	0.331–0.436
	0.017	0.015	0.016	0.035	
Primary growth rate	3.28	3.44	3.45	3.39	3.02–3.60
(mm/day)	0.07	0.06	0.07	0.16	
Body mass of young	11.91	12.49	12.54	12.33	11.34–13.16
on day 14 posthatch	0.43	0.69	0.27	0.56	

[a] Within each cell of the four rows on the left, the upper number is the mean and the lower number is the standard deviation.

[b] Reproductive success = fledglings/eggs.

growth constant (K) did not vary significantly among years or with brood size (ANOVA, $P > 0.2$). The nestlings in the later nests, however, grew significantly faster (regression on the date of the first egg, b = +0.005, $P = 0.011$, constant K = 0.213 + 0.005 date; Fig. 1). Body mass of nestlings on day 14 posthatch did not vary significantly among years (Table 1) or with date of first egg (ANOVA, $P > 0.2$). However, day-14 body mass appeared to be related to brood size; nestlings in smaller broods were heavier (regression on the brood size, b = −0.163, $P = 0.064$, N = 13, mass = 13.4 − 0.163 brood size). Body mass of fledglings was not significantly related to their growth rate (regression, $P = 0.80$). The growth rate of the fifth primary varied similarly with the growth constant, K. Feather growth was not significantly affected by either year or brood size (ANOVA, $P > 0.2$), but the nestlings in later broods tend to grow their fifth primary faster (regression on the date of the first egg, b = 0.017, $P = 0.082$, N = 13, rate = 2.83 + 0.017 date).

Males made significantly more feeding trips to nest than did females (paired t-test, $t = 3.56$, N = 8 nests, $P = 0.009$, Fig. 2). Females increased the number of feeding trips per brood as brood size increased (Regression, b = 0.82, $P = 0.046$, N = 8 broods, number of trips = 1.18 + 0.82 brood size), while total number of visits and number of visits by males per nest were not significantly affected by brood size ($P > 0.2$, calculated

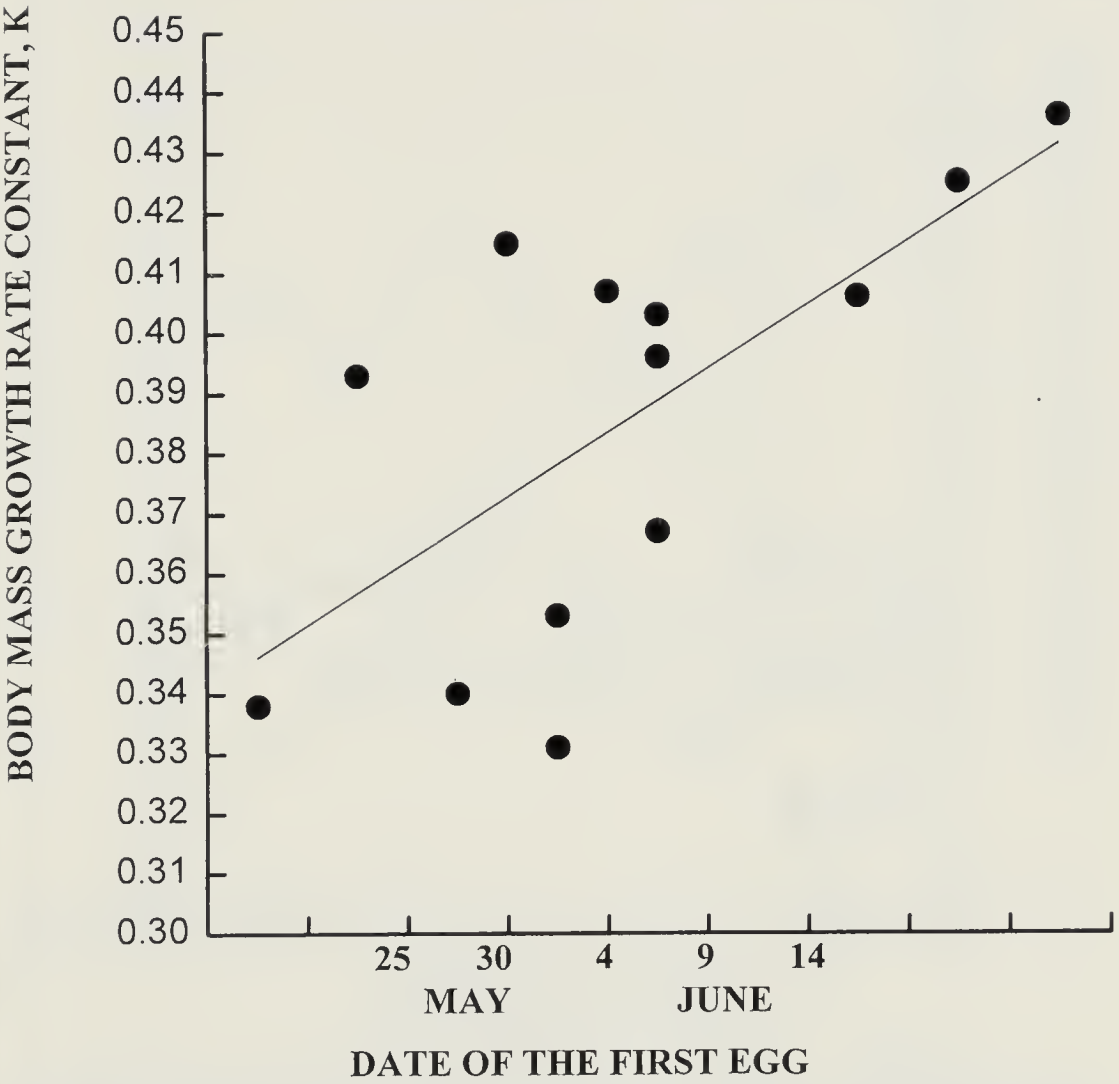

FIG. 1. Relationship between body mass growth rate constant, K, of Willow Tits and the date of the first egg.

on averages per nest for the entire nestling period). GLM analysis using all feeding observations and brood as a factor during the entire nestling period showed no significant relationships between the number of visits per nest (total, male and female separately) and brood size ($P > 0.2$). Both total number of visits per nest (slope = 3.12, $P < 0.01$) and number of visits by females (slope = 3.95, $P < 0.01$) significantly increased as nestlings grew older, although male feeding rate was affected by nestling age only suggestively (slope = 1.56, $P = 0.095$). The number of feeding trips per young (total, male and female separately) was also not significantly affected by brood size ($P > 0.4$, calculated both for nest averages for all nesting period and with a nest as a factor for all feeding observations). Both total number of feeding trips (GLM with a brood as a

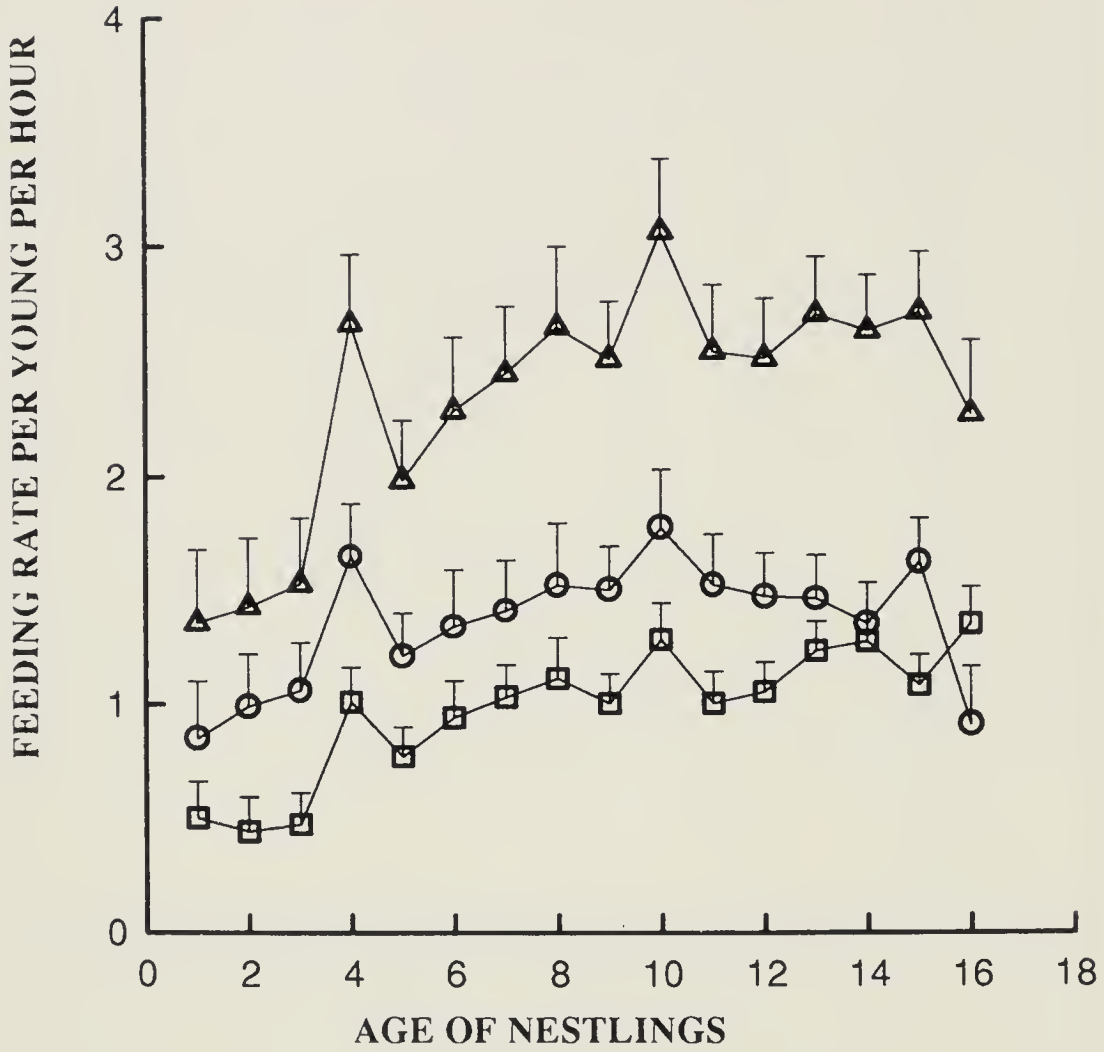

FIG. 2. Number of feeding visits of Willow Tits per nestling per hour as related to nestling age. Open circles and squares represent feeding rates of males and females, respectively. Triangles represent rates for males and females combined. Vertical lines represent ± one SD of the means.

factor, slope = 2.64, $P < 0.01$) and number of visits by female per young (slope = 3.30, $P < 0.01$) increased significantly as nestlings grew older, while male feeding rate was not significantly affected by nestling age (slope = 1.29, $P = 0.22$). Since some young left their nest on the 14th day posthatch and nestling body mass (Fig. 3) and parental feeding rate (Fig. 3) started slowing down by the 13th day posthatch, we analyzed the frequency of parental feeding visits separately for the first 13 days of nestling age (N = 116 1-h periods for 8 nests). This separate analysis of the first 13 days may be very important since the young reach their fledging body mass and are able to fledge by that time, so the heaviest pressure on parents should fall in this period. The results were strikingly different

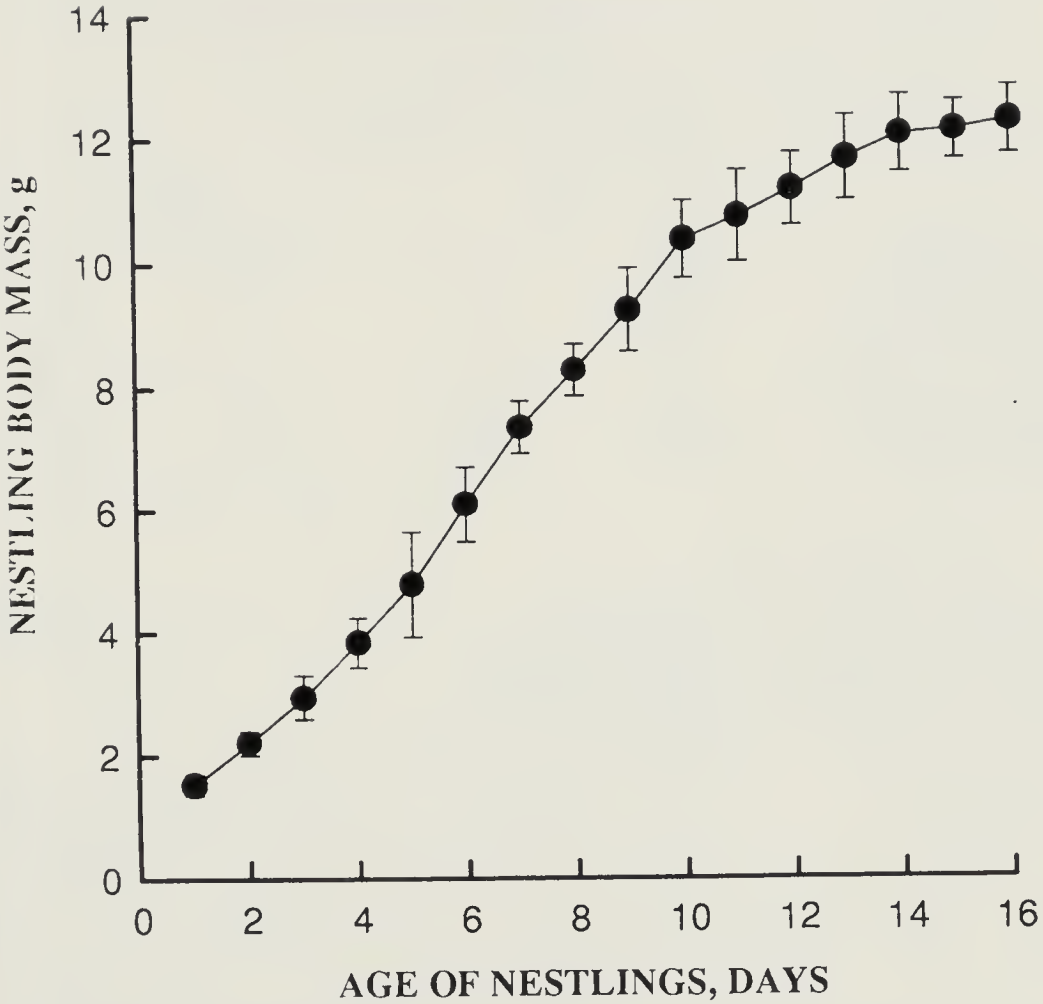

FIG. 3. Nestling body mass of Willow Tits as related to nestling age.

from those of the whole nesting period (Table 2). Both total number of feeding trips and number of feeding trips by female per brood and per young increased significantly as nestlings grew older. Male feeding rate, though, did not change significantly with nestling age (Table 2). Both males and females increased number of feedings per nest as brood size increased. Feeding frequency per young showed a dramatic difference between sexes (Fig. 4). Females made more feeding trips per young in larger broods, while males made significantly fewer of them as brood size increased (Table 2, Fig. 4).

Females, but not males, spent more time attending nests containing fewer young during the entire nesting period (GLM with nest and brood size as factors, $F_{2,579} = 8.27$, $P < 0.001$). Both male and female decreased their attendance time as nestlings grew older (GLM with a nest as a factor, $P < 0.01$, Fig. 5).

Arachnoidea, Lepidoptera, and Diptera comprised the majority of the

TABLE 2

RELATIONSHIPS BETWEEN PARENTAL FEEDING RATE AND NESTLING AGE (DAY 1–13) AND BROOD SIZE IN THE WILLOW TIT

	Age		Brood size	
No. of visits/h	Slope	*P*	Slope	*P*
Male per brood	0.16	0.13	1.10	0.00
Female per brood	0.44	0.00	1.37	0.00
Total per brood	0.59	0.00	2.49	0.00
Male per young	0.03	0.11	−0.12	0.01
Female per young	0.06	0.00	0.08	0.01
Total per young	0.09	0.00	−0.03	0.58

nestlings' diet (79%, Tables 3 and 4). The number of prey items contained in each individual food load brought to nestlings averaged 3.0 and did not vary significantly among years ($F_{1,8} = 1.76$, $P = 0.23$, Table 5) or different broods (no two pairs were different at $P = 0.05$, Tukey's test). Average mass of a load taken during 1989–1990 also was not statistically different (*t*-test, $t = 1.74$, $P = 0.22$, N = 7) between these years (Table 3), although there were significant differences among broods during both years (in 1989, one nest was different from one out of 3 broods and in 1990, one nest was different from the rest, all differences at $P = 0.05$, Tukey's test). The mass of a food load was positively and significantly related to the number of prey items in a load when differences among years and broods were accounted for (ANCOVA with year and brood as factors and the number of items in a load as a covariate, individual load is the primary sampling unit; slope = 15.64, $t = 5.49$, $P < 0.001$). Even though all major prey items showed a great deal of variation there were no significant difference in average frequency of any major prey type per load either among years or among broods (no pairs compared were different at $P = 0.05$, Tukey's test).

DISCUSSION

The breeding biology of the Willow Tit in northeastern Siberia and western Europe appears to be very similar (Orell and Ojanen 1983). Average clutch size (7.62) and number of fledglings (6.19) in Finland (Orell and Ojanen 1983) are nearly identical to those in Siberia (7.5 eggs and 6.5 fledglings). The trend toward reduced clutch size with later breeding seems to be general not only for Willow Tits but for many other bird species as well (Orell and Ojanen 1983). Nestling growth rate (K) of Siberian Willow Tits (0.331–0.436) is very similar to that of Willow Tits

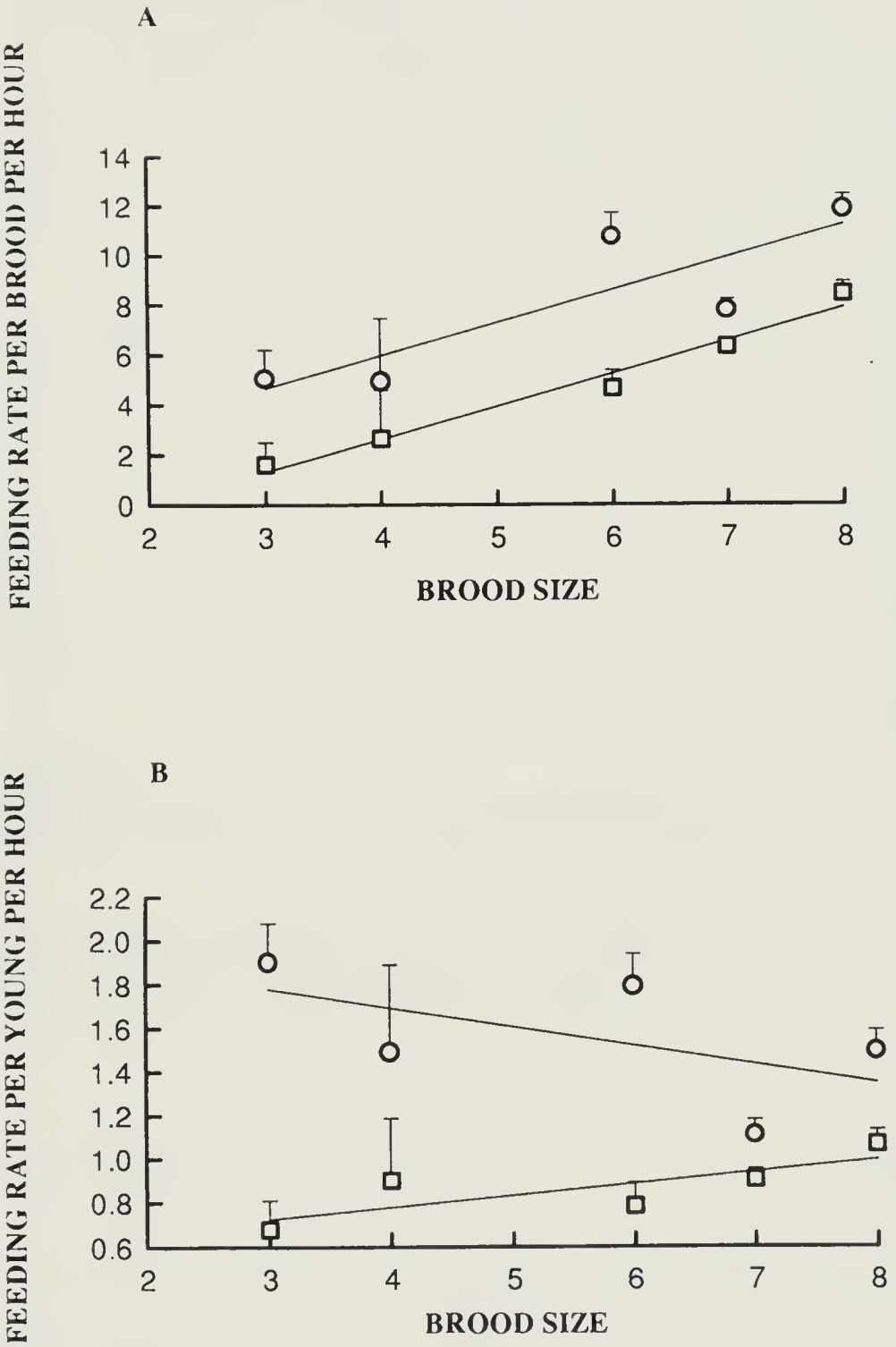

FIG. 4. Feeding rates by male and female Willow tits per brood (A) and per nestling (B) as related to brood size. Feeding rates are taken as averages for the first 13 days of nestling age, and lines represent standard deviations of the means. Males are represented by circles and females by squares.

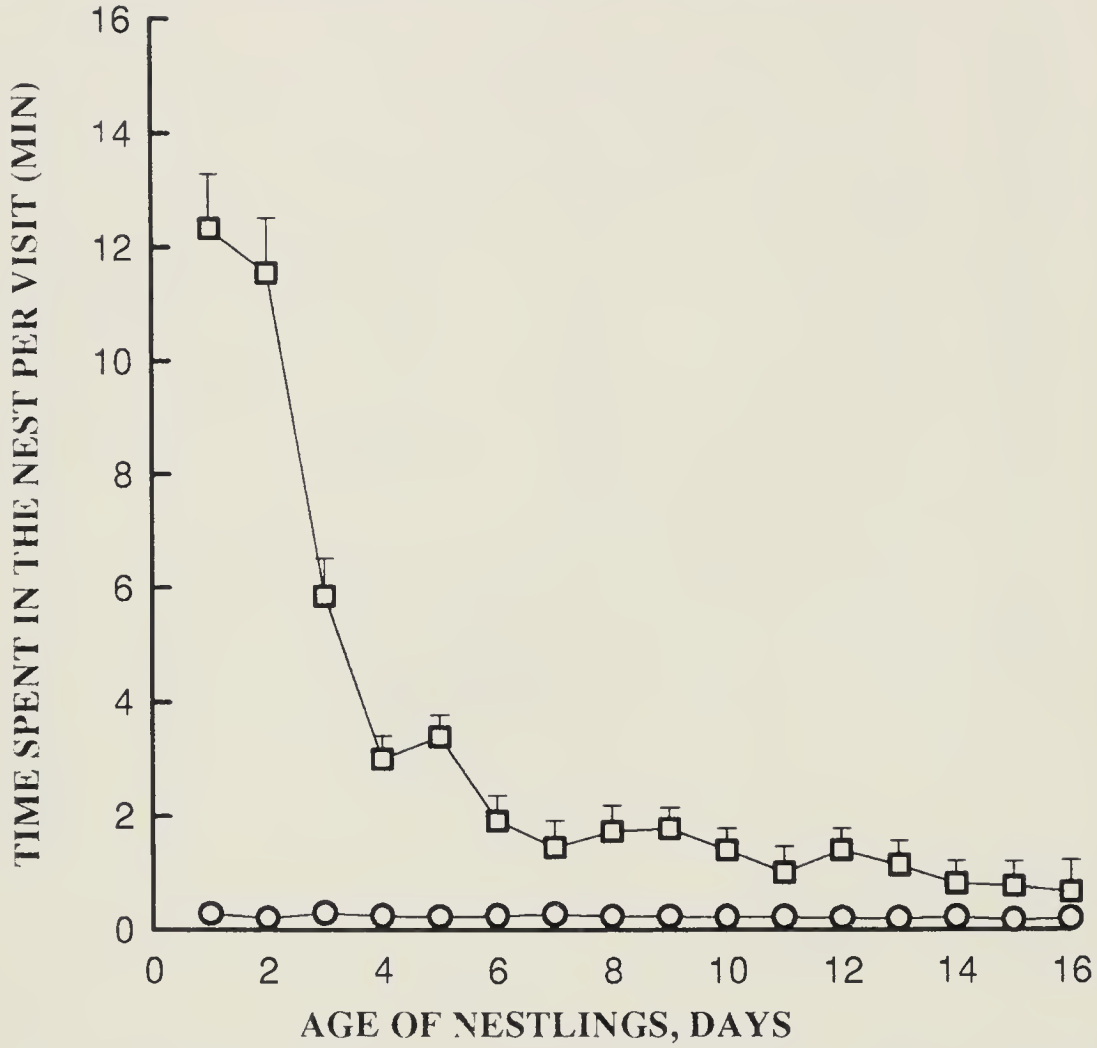

FIG. 5. Length of time spent in the nest cavity during one visit by male and female Willow Tits as related to nestling age. Vertical lines represent standard deviations of the means. Males are shown by circles and females by squares.

in other studies (0.380–0.406; Foster and Godfrey 1950, Inozemtsev 1962, Song 1980, Orell and Ojanen 1983). The negative correlation between fledgling body mass and brood size has also been demonstrated before (Nur 1984, Orell and Koivula 1990).

It seems that birds that start breeding earlier typically produce more fledglings. However, we found that nestling growth rate was positively correlated with the start of breeding. Nestlings that hatched later grew significantly faster although there was no effect of the timing of breeding on fledgling body mass. The fledgling body mass was also unrelated to their growth rate. This result may suggest that although late-breeding pairs produce fewer fledglings, their young could be better off nutritionally. Timing of breeding has long been thought of as a life-history trade-off.

TABLE 3

FREQUENCY OF DIFFERENT FOOD TYPES IN THE DIET OF NESTLING WILLOW TITS IN SIBERIA

Prey taxon	1987	1989	1990	Total	Percent
Arachnoidea	9	20	20	49	16.5
Total Lepidoptera	25	63	45	135	45.6
Larvae	18	59	45	122	41.2
Imago	7	4	0	13	4.4
Total Hymenoptera	15	3	2	20	6.8
Larval Hymenoptera	0	2	0	2	0.7
Tentridinidae	1	0	0	1	0.3
Pamphilidae	0	1	0	1	0.3
Formicidae	1	0	2	3	1.0
Total Coleoptera	16	4	2	22	7.4
Larval Coleoptera	15	2	2	19	6.4
Diptera	38	10	2	50	16.9
Limoniidae	25	0	0	25	8.4
Tipulidae	10	9	2	21	7.1
Unidentified	3	1	0	4	1.3
Plecoptera	2	4	0	6	2.0
Chloroperlidae	0	3	0	3	1.0
Unidentified	2	1	0	3	1.0
Homoptera	1	2	0	3	1.0
Gastropoda	0	1	1	2	0.7
Fish bones	2	0	0	2	0.7
Total number	111	114	71	296	

Birds may benefit by breeding earlier, possibly because food abundance is higher. However, for the Willow Tits breeding in Siberia, this is probably not true since when they start breeding there is still snow cover and food becomes abundant only later (pers. obs.). Other studies have shown that in some resident passerine birds, including the Willow Tit, there is another important benefit from breeding earlier; young fledged earlier stand a better chance of recruitment into both winter flocks and into the next season's breeding population (Nilsson 1988, Koivula et al. 1993, Pravosudov 1993b). Our results suggest that there may be a trade-off between early and late breeding in the Willow Tit. If nutritional condition of fledglings were independent of the start of breeding, birds breeding earlier would produce young that would have a higher chance of establishing themselves into a subsequent breeding population. However, birds breeding later may produce better nourished young, although fewer of them. The optimal time of breeding may thus reflect a trade-off between breeding early enough to produce early dispersers (and successful recruits) and breeding late enough to produce well nourished young.

TABLE 4

MASS (MG) OF DIFFERENT FOOD TYPES IN THE DIET OF NESTLING WILLOW TITS

Prey taxon	1989	1990	Total	Percent
Arachnoidea	833	702	1535	20.5
Lepidoptera	2392	2531	4923	65.8
Larvae	2175	2531	4706	62.9
Imago	217	0	217	2.9
Hymenoptera	160	85	245	3.3
Pamphilidae	60	0	60	0.8
Formicidae	0	85	85	1.1
Larvae	100	0	100	1.3
Coleoptera	57	104	161	2.1
Larvae	36	104	140	1.9
Diptera	310	119	429	5.7
Tipulidae	290	119	409	5.5
Plecoptera	84	0	84	1.1
Chloroperlidae	68	0	68	0.9
Homoptera	76	0	76	1.0
Gastropoda	16	14	30	0.4
Total	3928	3555	7483	

Parental behavior in which male Willow Tits fed young more often than females but females spent more time attending nestlings during the whole nesting period was quite similar to that of the Mountain Chickadee (*Parus gambeli*) (Grundel 1987). However, during the first 13 days of nestling life, Willow Tits differed significantly from Mountain Chickadees in the way the sexes responded to changes in brood size. In our study, both males and females increased the number of feeding visits per brood as the brood size increased. However, the number of feeding trips per young was negatively correlated with brood size in males but positively correlated in females. This result, and also the fact that male feeding rate

TABLE 5

MEASUREMENTS OF NESTLING FEEDING IN THE WILLOW TIT

Parameter	1987	1989	1990	Total
Number of loads	24	49	35	108
Number of broods	4	4	3	11
Number of food items/load	4.2 (2.6)[a]	2.2 (0.7)	2.5 (0.8)	3.0 (1.8)
Mass of a food load	—	81.1 (22.2)	127.9 (42.4)	101.1 (38.4)

[a] SD.

did not change much with nestling age, may indicate that males worked as hard as possible and that is why their feeding rate was similar for broods of different size and age throughout the entire nesting period. On the other hand, females appeared to adjust their feeding rate to variation in demand caused by different ages of young and different brood sizes. Females, but not males, also adjusted their attendance time to brood size while feeding nestlings.

It is known that parental feeding rate by itself is not necessarily a good indicator of parental investment since the biomass of food brought by parents to their young per visit may differ between males and females (Grundel 1987). However, Grundel (1987) found in the Mountain Chickadee that differences in total volume of food per nestling in broods of different size were due to changes in feeding frequency rather than in prey size or load size. Therefore, the patterns of feeding frequencies by male and female Willow Tit parents of large and small broods appear to be a valid representation of their investment. The pattern of feeding rate with an increase in the beginning of the nestling stage, a plateau in the middle, and a decrease before fledging seems to be very common and has been shown for many parids (Gibb 1950, Royama 1966, Grundel 1987). Because of the sexes' opposite trends in feeding rate per young with an increase in brood size, the total number of feedings per young in Siberian Willow Tits was not significantly different in broods of different size. This pattern has not been found in many studies (Gibb 1950, 1955; Royama 1966, Walsh 1978, Grundel 1987), although it has been demonstrated before (Pinkowski 1978). Assuming that the changes in feeding rate associated with changes in brood size truly represent a change in parental investment, our results are consistent with the individual adjustment hypothesis (Hogstedt 1980, Pettifor et al. 1988) which assumes that birds adjust their clutch size to their own capabilities of raising young. The absence of any relationship between brood size and nestling growth rate also appears to support this hypothesis. The negative relationship between fledgling body mass and brood size seems to go against the individual adjustment hypothesis since post-fledging survival is known to correlate positively with fledging body mass (Nur 1984, Orell and Koivula 1990). Since young in large broods tend to be lighter compared with young from smaller broods, one can assume that those from larger broods should have lower survival. However, experimental results from studies of Willow Tits in Finland did not fully support this assumption, suggesting that any relationship among brood size, nestling weight, and juvenile survivorship can be complicated by environmental variability (Orell and Koivula 1990). Also, from all the relationships described above, we can assume that lighter young fledge earlier (earlier breeding start results in

larger brood size which results in lighter body mass of fledglings) and, if they survive, would have a greater chance of breeding.

ACKNOWLEDGMENTS

We thank Elena Zimireva for her assistance in the field. T. C. Grubb, Jr., R. A. Mauck, and T. A. Waite, O. Hogstad, and C. R. Blem provided valuable comments on an earlier draft of the manuscript.

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CENSUSING WINTERING POPULATIONS OF SWAINSON'S WARBLERS: SURVEYS IN THE BLUE MOUNTAINS OF JAMAICA

Gary R. Graves

Abstract.—Census methods developed for breeding populations of Nearctic-Neotropic migrant passerines are largely ineffective for determining the distribution and abundance of Swainson's Warbler (*Limnothlypis swainsonii*) on its wintering grounds in the Caribbean basin. Using playback of tape-recorded call notes interspersed with advertising songs, I found the warbler to be widespread and relatively common in montane forests of the Blue Mountains of Jamaica. Detection rates with playback varied from 17.8 to 29.2 warblers/10 h along five census transects. Census efficiency was increased by an estimated factor of five to 10 times with the use of tape playback. *Received 23 March 1995, accepted 20 Aug. 1995.*

For conservationists, the apparent decline of some Nearctic-Neotropic migratory birds is a serious concern (Terborgh 1989, Robbins et al. 1989) that demands both rigorous management and quantitative monitoring of breeding and wintering populations. Effective census techniques have been developed for many songbird species (Passeriformes) during the breeding season (Ralph and Scott 1981, Robbins et al. 1986). However, songbirds rarely sing on their wintering grounds and during fall migration, are feathered in duller basic plumages, and hence, are more difficult to detect and identify than during the breeding season. Yet most studies of migrants in the Neotropics employ censusing techniques designed for breeding birds of higher latitudes, with little or no attempt to compensate for the decreased detectability of wintering populations. As this report will communicate, standard point count and transect censusing methods can be relatively ineffective in determining the true abundance of secretive migratory species that winter in dense tropical habitats.

The breeding and wintering biologies of Swainson's Warbler (*Limnothlypis swainsonii*) are among the most poorly known of the migratory wood warblers (cf Meanley 1971, Eddleman 1978, Graves 1992, Brown and Dixon 1994, Thomas 1994). Wintering birds have been reported in the Caribbean basin from the Bahamas, Cuba and the Isle of Pines, Jamaica, Cayman Islands, and the Yucatan Peninsula, casually east to Puerto Rico and the Virgin Islands, and from southern Veracruz south to Honduras (Meanley 1971, AOU 1983, Pashley 1988, Winker et al. 1992). Most wintering records are anecdotal (e.g., Eaton 1953), and, at present, wintering sites where more than one or two individuals can be consis-

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tently encountered per day are known only from certain regions of Cuba (G. Wallace, pers. comm.; Kirkconnell et al., unpubl. ms.). This paper documents the utility of playback techniques for censusing wintering populations of Swainson's Warbler and reports the discovery of what appears to be a major wintering area for the species in the Blue Mountains of Jamaica.

METHODS

Study area.—I surveyed Swainson's Warbler populations along the same trails and roads at Hardwar Gap that were studied by the Lacks, from 2 to 10 February 1995. Hardwar Gap, at the divide forming the boundary between St. Andrew and Portland Parishes in the Port Royal Mountains (an outlier of the Blue Mountains), is accessible along a hard-surfaced road (B1) from Kingston to Buff Bay on the northern coast. Hardwar Gap is one of the most frequent destinations in Jamaica of resident and visiting ornithologists and bird watchers. Both Hardwar Gap and the adjacent Hollywell Park now lie within the borders of the Blue and John Crow Mountains National Park (Muchoney et al. 1994).

Three census transects were established along trails ("forest" transects in Table 1) that pass through a peninsula of upper montane rain forest connected to a much larger block of forest eastward in the national park (see Asprey and Robbins 1953 and Muchoney et al. 1994 for descriptions of habitat). The Hardwar Gap region was extensively affected by Hurricane Gilbert in 1988 (Wunderle et al. 1992), and patches of early successional vegetation were present along all three forest transects, but there was little evidence of cutting or other human disturbance away from roadsides. Transect terrain was extremely steep. Slopes varied from 15° to 70° and were estimated to average over 40°. Significant portions of forest trail No. 3 (Table 1) were at the summit of a knife-like ridge.

The fourth and fifth census routes followed the main road (B1) from a point just below Hardwar Gap to the village of Section, Portland Parish. This road forms the boundary between relatively undisturbed montane forest (upslope) and a patchwork of lightly modified montane forest, coffee plantations, residential gardens, and agricultural scrub (downslope) in the 1 km buffer zone of the national park. The upper and lower sections of the road, although contiguous, were treated as separate census routes (Table 1).

The length of "forest" transects was estimated by averaging the number of steps counted on three downslope trips (at 0.76 m/step). The road transects were measured with a vehicle odometer. Elevations were estimated by multiple readings of a calibrated altimeter.

Census methods.—I used techniques developed for monitoring breeding populations of Swainson's Warblers in the southeastern United States (Graves, unpubl.). Loop cassette tapes (20 s and 60 s) were prepared from recordings (made a with Marantz PMD430 cassette recorder and a Sennheiser ME 80 directional microphone in Virginia and Louisiana) of Swainson's Warbler call notes interspersed with a primary song every 15 s (one song on 20 s loop). Advertising songs were included because they are more easily heard above the low frequency noise caused by rustling leaves and dripping water in the forest understory. The opposite proportion of songs and calls are used to census breeding populations.

Recordings were broadcast from a dual-speaker "boom box" (Sanyo). Power output was variable due to battery use and atmospheric conditions, but the audio output was adjusted before every census run so that call notes were audible to me at a distance of 60 m and songs at a somewhat greater distance (unobstructed by vegetation). The direction of the speakers was rotated every 5 to 10 s until a probable response was detected. During clear weather at Hardwar Gap, Swainson's Warblers responded to tape broadcasts from distances

TABLE 1

CENSUSES OF SWAINSON'S WARBLERS AT HARDWAR GAP, BLUE MOUNTAINS, JAMAICA

Census transect	Census run	Starting time	Census duration (m)	Weather[a]	Number recorded	Cumulative number
Forest trail no. 1[b]	1	15:30	45	PC, O, F	1	1
	2	06:55	120	PC, F	2	2
	3	14:27	68	C	4	4
					[c]18.0 warblers/10 h	
Forest trail no. 2[d]	1	07:14	40	C	2	2
	2	07:55	69	C, PC	3	4
	3	16:21	33	C	0	4
	4	16:55	54	C, PC	2	4
	5	13:21	50	O, F	1	4
	6	14:15	45	O, F	1	4
					18.6 warblers/10 h	
Forest trail no. 3[e]	1	12:02	98	O, M, R	1	1
	2	13:40	84	M, R	1	2
	3	13:18	92	O, F	6	6
	4	14:52	73	F, R	2	6
	5	07:16	178	C	6	10
	6[f]	10:30	70	C, PC	7	12
					23.2 warblers/10 h	
Road (upper)[g]	1	07:05	190	PC	8	8
	2	10:22	98	PC	7	11
	3[f]	10:00	60	O, PC	2	13
					29.2 warblers/10 h	
Road (lower)[h]	1	07:38	54	F, M, R	1	1
	2	08:35	57	F, M, R	1	2
	3	11:31	69	F, M	1	3
	4	12:42	70	F, M	1	3
	5	06:45	72	O	6	8
	6	07:58	84	O	2	9
					17.8 warblers/10 h	

[a] F = heavy fog; M = mist; R = rain; O = overcast; PC = partly cloudy; C = clear.
[b] Length = 1604 m; elevation = 1140–1200 m.
[c] Total number of warblers recorded over all census runs standardized by duration of censuses.
[d] Length = 530 m; elevation = 1140–1200 m.
[e] Length = 1808 m; elevation = 1140–1325 m.
[f] Playbacks only at significant distributional gaps (at distances >150 m from nearest flagging marker).
[g] Length = 2980 m; elevation = 990–1140 m.
[h] Length = 1409 m; elevation = 945–990 m.

as great as 80 to 90 m (usually upslope or downslope). Response was significantly curtailed during periods of heavy mist and rain, probably because the effective range of the tape broadcast was attenuated by noise.

After a warbler responded and its location was marked with plastic flagging, I walked quietly from the area until I could no longer hear the calling bird (80–90 m during clear weather), at which point I resumed playback. Otherwise, tape playback was continuous and only intermittently stopped to listen for suspected responses.

Territory size in wintering Swainson's Warblers is unknown. "Playback-and-follow" trials were performed on more than a dozen individuals. Five warblers followed the playback more than 50 m (66, 80, 113, 119, 122 m, respectively) from the initial point of response (measured from a point perpendicular to the trail or road). Judging from this evidence and the relatively large size of breeding territories (Graves 1992, unpubl. data), I conservatively considered any subsequent response within 150 m of the original discovery point to refer to the same bird unless two or more individuals were heard calling simultaneously in the zone. When in doubt, I attempted to determine the approximate territorial boundary with "playback-and-follow" trials. When a warbler's territorial boundaries were reasonably understood, playback on subsequent census runs in that territory was halted after a response was elicited.

RESULTS

Behavioral responses of Swainson's Warblers to tape playback were variable, ranging from close approaches (4–5 m) to the observer and frequent back-and-forth flights accompanied by vigorous calling, to a subdued approach (8–14 m) accompanied by a few faint chips and ventriloquial "seep" notes, following by rapid disappearance (within 30 s) of the warbler.

On several occasions, vigorous responses often elicited counter-calling from other individuals in adjacent territories (N = 5 different "counter-calling" pairs). In one case, a highly agitated Swainson's Warbler flew across the road only to be promptly attacked by a counter-calling bird. Only once did a warbler respond to playback by giving a primary song (three somewhat incomplete renditions). Although my observations in each territory were necessarily brief, no evidence of territorial overlap or pairing was observed. The intense border displays and skirmishes observed are the first evidence of intraspecific territoriality of Swainson's Warbler on its wintering grounds (cf Eaton 1953). With the exception of the single warbler that sang (presumably male), the sex of individuals was unknown. However, the timid vocal and behavioral responses of some warblers were similar to the behavior of females on breeding territories (Graves, unpubl. data).

Interspecific responses of other wintering wood warblers at Hardwar Gap to Swainson's Warbler call notes and songs were variable. Vigorous counter-calling was elicited from the Ovenbird (*Seiurus aurocapillus*). Common Yellowthroats (*Geothlypis trichas*) frequently approached the speakers and counter-called, and the single Louisiana Waterthrush (*Seiu-*

rus motacilla) encountered during the censuses approached from a distance of >50 m along a stream channel and called. More subdued responses were recorded for Black-throated Blue Warbler (*Dendroica caerulescens*), Black-and-white Warbler (*Mniotilta varia*), American Redstart (*Setophaga ruticilla*), and Worm-eating Warbler (*Helmitheros vermivorus*). The few Prairie Warblers (*D. discolor*) encountered along the road transect and in bracken-dominated swards appeared to exhibit little interest in Swainson's Warbler playback.

Forty-two Swainson's Warblers (68 census records) were recorded on the five census transects. The number of detections ranged from four to 13 warblers/transect (Table 1), and relative abundance varied from 2.13 to 7.77 warblers/km. Playback of taped calls and songs was instrumental in detecting and mapping the locations of individuals. Call notes were heard on only four occasions when playback was not being used. Detection rates were consistently high under clear or overcast skies, but were markedly lower during periods of heavy mist and light rain or immediately afterwards (e.g., forest trail no. 3: census runs 1, 2, and 4 vs 3, 5, and 6). In general, a minimum of three or four census runs under clear or overcast skies was necessary to locate and map Swainson's Warbler territories along each census transect.

Rates of Swainson's Warbler detection along the five transect segments (Table 1) varied from 17.8 to 29.2 warblers/10 h. Because of territorial spacing, the number of individuals recorded along a transect is clearly influenced by its length and the spatial distribution of high-quality habitat. A few tentative comparisons can be made between my data (Table 1) and Lack's (1976: appendices 19 and 20), assuming our rates of movement (0.5–2.1 km/h vs. slow walk) were similar. Lack's "slow walk" censuses through montane forests yielded three Swainson's/10 h (N = 32 h of censuses) but none (N = 12 h) along roadsides at Hardwar Gap. Comparable figures with playback ranged from 18.0 to 23.2 Swainson's Warblers/10 h (N = 18.7 h of censuses) along forest trails and from 17.8 to 29.2 warblers/10 h (N = 12.6 h of censuses) along roadsides. The contrast between the Lacks' and my roadside data are particularly striking.

Wunderle et al. (1992) failed to detect Swainson's Warbler with fixed-radius point count censuses in montane forest at Hardwar Gap either before (December 1987) or after (January 1989) Hurricane Gilbert. Based on my observations and previous work at Hardwar Gap (especially that of the Lack's 1972, 1976), I estimate that the use of playback is five to ten times more efficient than standard point count or transect methods for censusing wintering Swainson's Warblers.

I estimated that tape playback of Swainson's Warbler calls and songs sampled a path approximately 150 m wide along census transects in the

Hardwar Gap area. Detectability is a function of territory placement. The farther a territorial boundary is from the transect, the less likely the occupant will be detected, with or without tape playback. Thus, the cumulative totals in Table 1 represent estimates of the *minimum* number of warblers along each transect.

Mist-netting studies are likely to be less efficient in determining the distribution and abundance of wintering Swainson's Warblers. Because Swainson's Warblers appeared to be territorial and birds were dispersed in the Blue Mountains (2.13 to 7.55 warblers/km of transect), mist nets would have to be scattered widely to capture more than a few resident birds, regardless of the number of net hours. Winter foraging behavior appeared to be remarkably similar to that observed during breeding season (Graves, unpubl. data; see Lack 1976). All foraging motions of Swainson's Warblers observed during February 1995, were directed toward dead leaves, most often in the leaf litter, but also toward dead leaves on fallen logs or inclined tree trunks within 1.5 m of the ground. Undisturbed birds rarely flew more than a few meters and usually close to the leaf litter. If observations from breeding territories might serve as a guide, foraging Swainson's on their wintering territories may walk up to mist nets, appear to inspect the linear net lane and the net itself, and then proceed to walk under or around them. The consequence of large and dispersed territories combined with a terrestrial mode of foraging produce low rates of mist-net capture, even when the habitat is "saturated" by wintering birds. In any event, a large area (ca 100 ha) that would require hundreds of man hours to sample adequately with mist nets may be efficiently censused with playback in one or two days by a single observer.

As a note of caution, density estimates cannot be calculated from data in Table 1. Sections of the census transects were bordered by habitat that appeared to be unoccupied by Swainson's Warblers in the Hardwar Gap area (e.g., bracken-dominated swards along forest transects; coffee, residential gardens, landslides, and agricultural scrub along the road). Transect data also need to be corrected for "switch-back" or "hair-pin" sampling. This situation occurs when census transects switch directions abruptly and the same area is sampled one or more times by the playback broadcast. Wintering density at Hardwar Gap can be estimated only after habitat patchiness and "hair-pin" sampling are accounted for (Graves, unpubl. data).

In summary, Swainson's Warblers appeared to be a widespread and relatively common wintering resident in undisturbed and slightly modified montane forest in the Hardwar Gap region of the Blue Mountains. At present, more than 50,000 ha of apparently suitable habitat occurs within the borders (including buffer zone) of the Blue and John Crow Mountains

National Park (Muchoney et al. 1994). If Swainson's Warbler densities are relatively uniform throughout this montane region, the park may support 17,000–25,000 wintering individuals (Graves, unpubl. data). Regardless, the 42 individuals found at Hardwar Gap constitute the largest known wintering population of Swainson's Warbler.

DISCUSSION

History and status of Swainson's Warbler in Jamaica.—The distribution and abundance of Swainson's Warbler in Jamaica is inadequately known, perhaps owing to its secretive behavior and cryptic appearance. The first specimen from Jamaica was collected by Edward Newton at Hope, St. Andrew Parish, on 8 February 1879 (Newton 1879). This specimen was the first of a series of eight collected by Newton from 1 October to 8 April (1879–1882) at Hope, Hermitage, and Mt. Elizabeth, St. Andrews Parish, and at Port Royal, St. Thomas Parish (Merriam 1885). Bond (1940) overlooked Merriam's paper and referred implicitly to Newton's first specimen as the only record for the island. Five years later, Bond (1945:118) noted that Swainson's Warbler "winters in Jamaica (at least nine records from October 1 to April 8)."

Foreshadowing the findings of Lack some twenty years in the future, Tordoff (1952:321) reported, "I collected three female Swainson's Warblers in the winter of 1946–47 . . . within 15 miles of Kingston. In addition, I saw at least nine others between December 31 and February 7. On two occasions I saw three in one day. My observations indicate that this warbler winters in Jamaica in fair numbers. Six of the individuals that I saw were in dry lowland woods; the rest were in damp forests in the hills north of Kingston (at Hermitage, St. Andrew Parish)."

In the early 1970s, Lack (1976:174–175) found Swainson's Warbler to be "regular in lowland woods and montane forest with thick undergrowth, and also in the tall dark forest with a dense canopy but no undergrowth." Lack recorded 1–3 birds/10 h of observation in dry limestone forest near sea-level at Morant Point and Negril, in arid ruinate forest on Long Mountain, and in rich secondary forest in the Ferry River valley and Mona Wood. In montane forest at Hardwar Gap in the Blue Mountains, he observed three Swainson's Warblers/10 h on slow walks, and six warblers/10 h on fast walks along forest trails, but none along the roadside edges of the forest. Lack also noted that five Swainson's were banded but none was observed in the overgrown gardens at Greenhills, about 1.5 km ENE of Hardwar Gap in Portland Parish.

Compilations of the Gosse Bird Club (1963–1993) indicate that Swainson's Warbler was banded (cumulative total of 25 individuals) or observed nearly annually from 1963 through 1977, most frequently at Mona Woods

near Kingston (see Diamond and Smith 1973). The last published record for Jamaica in the 1970s was reported from the Blue Mountains in October 1977. Inexplicably, there were no additional published reports of Swainson's Warbler in Jamaica during the next 15 years until December 1992.

Three recent unpublished observations have come to my attention. Peter Marra (pers. comm.) banded 3–4 Swainson's Warblers on a 5-ha study site in dry limestone forest at Kew Park, Westmoreland Parish. Russell Greenberg (pers. comm.) observed one or two per day in the Hardwar Gap area during six days of field work in January 1984. Finally, Robert Sutton (pers. comm.) banded Swainson's Warblers at Greenhills in 1978, 1982, 1985, and 1986 (N = 10 individuals). In summary, the field studies of Tordoff (1952), and especially those of Lack and Lack (1972) and Lack (1976), combined with scattered sight and banding records compiled by the Gosse Bird Club (1963–1993), as well as the results of the present study suggest that Swainson's Warbler is a widespread wintering species occurring at low densities in Jamaica.

Conclusions.—The most significant recent advance in population studies of wintering songbirds or resident Neotropical species has been the use of tape-recorded playback of call notes and songs of focal species (e.g., Parker 1991). Among the wood warblers (Parulini; taxonomy of Sibley and Monroe 1990), tape playback has been used successfully to census Black-throated Blue Warblers in Jamaica (Holmes et al. 1989, Sliwa and Sherry 1992) and Puerto Rico (Wunderle 1992), American Redstarts in Jamaica (Holmes et al. 1989, Sliwa and Sherry 1992), Kentucky Warblers (*Oporornis formosus*) in Panama (Mabey and Morton 1992), and Hooded Warblers (*Wilsonia citrina*) in the Yucatan Peninsula (Lynch et al. 1985).

Swainson's Warbler may be added to the list of Nearctic-Neotropic migrants that are most effectively monitored on their wintering grounds with tape playback. Although playback census techniques are perhaps less crucial for wintering species that are behaviorally conspicuous and occupy open habitats (e.g., Palm Warbler [*Dendroica palmarum*]), results from the cited field studies suggest that censusing efficiency can be significantly enhanced for all wintering wood warblers with species-specific tape broadcast.

At Hardwar Gap, the entire wintering warbler fauna could be censused along the same census transects by including call notes of the nine most common species on a single loop cassette or audio compact disc (CD) Black-throated Blue Warbler ([*Dendroica caerulescens*], Prairie Warbler [*D. discolor*], Black-and-white Warbler [*Mniotilta varia*], American Redstart [*Setophaga ruticilla*]; Worm-eating Warbler [*Helmitheros vermivo-*

rus], Swainson's Warbler [*Limnothlypis swainsonii*], Ovenbird [*Seiurus aurocapillus*], Louisiana Waterthrush [*S. motacilla*], and Common Yellow-throat [*Geothlypis trichas*]). Extended cuts of particular species could be played as needed (cut selection on CD or separate loop cassettes). Tape broadcast of "spishing" noises, call notes of a single species, or owl calls, while better than nothing, are less effective in multi-species censuses of wintering warblers (Graves, unpubl.).

ACKNOWLEDGMENTS

I thank Russell Greenberg, Catherine Levy, Brooke Meanley, John Rappole, George Wallace, David Wiedenfeld, and Kevin Winker for insightful comments on the manuscript. Robert Sutton provided banding data. Logistics in Jamaica were greatly facilitated by David Smith and Susan Anderson (Jamaica Conservation and Development Trust, JCDT) and members of the Gosse Bird Club. Harold Thomas, Hyacinth Pascoe, and Dwight Pryce assisted my work at Hollywell. Permission to work in the Blue and John Crow Mountains National Park was granted by Franklin McDonald of the Natural Resources Conservation Authority. Field work was supported by the JCDT in cooperation with Smithsonian Institution.

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Wilson Bull., 108(1), 1996, pp. 104–114

COLONY-SITE AND NEST-SITE USE BY COMMON GRACKLES IN NORTH DAKOTA

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William J. Bleier,[1] and Robert B. Carlson[3]

Abstract.—We searched 638 quarter sections (0.8 × 0.8 km) for Common Grackle (*Quiscalus quiscula*) nesting sites in Benson County, North Dakota, in 1989 and 1990. We found 3596 active nests in 202 colonies on 177 quarter sections. Colonies in shelterbelts next to inhabited farmsteads were found at greater than expected frequencies ($P \leq 0.05$), whereas colonies in vegetation associated with potholes and miscellaneous habitats (woods, ravines, railroad easements, and lakesides) occurred below expected frequencies. Nest sites in stands of vegetation >100 m from farmstead residences occurred less frequently than expected ($P \leq 0.05$). Within colonies, nest sites in blue spruce (*Picea pungens*), Siberian elm (*Ulmus pumila*) and black poplar (*Populus nigra*) were found at greater than expected frequencies ($P \leq 0.05$) according to these species' availabilities, while green ash (*Fraxinus pennsylvanica*), American elm (*Ulmus americana*), and Russian olive (*Elaeagnus angustifolia*) were used below expected frequencies. The Common Grackle's preference for shelterbelts near inhabited farmsteads affected the physical and vegetative characteristics of colony sites and nest sites; with the exception of hawthorn (*Crataegus rotundifolia*), colonized stands had species compositions typically found in multi-rowed farmstead shelterbelts in North Dakota. *Received 7 Feb. 1995, accepted 25 Aug. 1995.*

The North Dakota population of breeding Common Grackles (*Quiscalus quiscula*) has more than doubled to 768,000 pairs (Nelms et al. 1994) from initial estimates made in 1967 (Stewart and Kantrud 1972). In the northern Great Plains, a region of intensive agricultural production, rows of shrubs and trees (shelterbelts) may be important nesting habitats for Common Grackles (Yahner 1982). In South Dakota and Minnesota, more than 50% of the birds nesting in multi-rowed shelterbelts were Common Grackles (Field 1971, Yahner 1982). North Dakota was historically dominated by prairie grasslands, and Common Grackles were restricted to nesting in the vegetation of riparian habitats, wetlands, and towns (Coues 1878). Recent plantings of numerous shelterbelts for agricultural and other purposes (e.g., insulation and beautification of farmsteads) may have enhanced the Common Grackle's access to prime nesting sites in North Dakota.

Records from the Comell Laboratory of Omithology indicate that coniferous and deciduous trees are most frequently used by grackles nest sites with 24% and 14% of the nests, respectively (Maxwell et al. 1976).

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However, quantitative comparisons of nest-site use by Common Grackles have been made only by Field (1971) and Yahner (1982). These studies involved nest-site use at the substrate level, and broader perspectives of colony-site use and habitat use were not investigated.

Our objectives were to determine habitat, colony-site, and nest-site use by Common Grackles in northcentral North Dakota. Our data on the preferred nesting sites of Common Grackles may benefit participants in shelterbelt-planting efforts (e.g., the North Dakota Centennial Tree Planting Project) who wish to avoid creating favorable nesting habitat for this species because it can damage crops.

STUDY AREA AND METHODS

Benson County is located in northcentral North Dakota in the northeastern Drift Plain Physiographic Region (Stewart 1975). The topography is flat to gently rolling, consisting of croplands interspersed with numerous potholes, temporary wetlands, and shelterbelts. The county is primarily cropland (74%). The remaining land area is dedicated to rangeland and pasture (17%) and woodlands, federal non-croplands, and other lands (9%). About 97% (5666 ha) of Benson County's native woodlands are in the east in the Devils Lake and Wood Lake regions. Water bodies > 16 ha represent 2% of the county. Siberian elm (*Ulmus pumila*) is the main species found in single-row shelterbelts. Multi-row shelterbelts consist of various combinations of species including Siberian elm, caragana (*Caragana aborescens*), green ash (*Fraxinus pennsylvanica*), boxelder (*Acer negundo*), plains cottonwood (*Populus deltoides*), and blue spruce (*Picea pungens*). In low-lying areas, willow (*Salix* spp.), quaking aspen (*Populus tremuloides*), and plains cottonwood grow naturally. Hawthorn (*Crataegus rotundifolia*), chokecherry (*Prunus virginiana*), and wild plum (*Prunus americana*) occur frequently in pastures and uncultivated areas. Large stands of bur oak (*Quercus macrocarpa*) are found in the hill region surrounding Devils Lake Basin.

Long-term average precipitation is 44 cm, with 72% of it falling in April–September (North Dakota Agricultural Statistics Serv. 1990). In May, the peak breeding period for Common Grackles in Benson County, the average temperature is 12°C. Average dates of first and last frosts (0°C) are 13 September and 23 May, respectively.

From 18 May through 10 June 1989–1990, we located active nests by systematic walk-through surveys on 638 randomly selected quarter sections (0.8 km × 0.8 km). All vegetation capable of supporting a Common Grackle nest was searched. Surveys were made daily from 09:00 to 18:00 h. A nest was considered active if it contained eggs, nestlings, or was defended by adults. An extendable pole with a mirror was used to check

for eggs and young. All nest sites were marked with colored mylar tape attached at the base of the nesting substrate.

We defined a nest site as the substrate on which a nest was built. A colony site was the stand of vegetation in which a nest occurred, with a stand being any continuous body of vegetation separated from all other such bodies by at least 50 m. We selected 50 m because colony sites were usually not defended at distances >50 m and thus could be considered distinct from other stands (Gutzwiller and Anderson 1987).

At each colony site, five nest sites and five potential nest sites (controls) were randomly selected. Controls included vegetation >1 m in height and capable of supporting a nest. The controls were selected by randomly drawing numbers and converting these numbers to meters on an *x*-*y* axis defined by the length and width of the colony site. If the coordinates did not fall on a suitable control, coordinates were redrawn until five controls were chosen. When ≤5 nest sites were present at a colony site, data were collected for all nest sites. We recorded plant species and trunk diameter at breast height (DBH), vegetation height, nest height, and distances to nearest permanent water (DPW) and residence (DRS) in 0–100, 101–300, 301–500, and >500 m categories. In 1990, we measured distance from nest sites to edge (DEG). Edge was defined as the border of any opening >5 m across where vegetation was ≤1 m. Heights of nests, nesting substrates, and controls were estimated with a telescoping pole or clinometer. Distance measurements >500 m were estimated with an optical range finder. A measuring wheel was used for distances <500 m.

If uncolonized stands were in a colonized quarter section (quarter), we gathered data from five controls allocated randomly among the stands. Typically, uncolonized stands were single-row shelterbelts of Siberian elm or low-lying areas dominated by willow, quaking aspen or plains cottonwood. If only one uncolonized stand was present, data for all five controls were drawn from this stand. Data were pooled across colonized quarters, and controls from uncolonized stands were compared against controls from the colonized stands.

Additionally, we made comparisons between colonized and uncolonized quarters. Controls from 70 uncolonized quarters that were surveyed for Common Grackles during 1989–1990 were compared against the combined controls from the colony sites and unused stands in the colonized quarters. Five controls were randomly selected from each of the colonized and uncolonized quarters.

Colony sites and uncolonized stands were classified according to the following habitats: inhabited farmstead shelterbelts, abandoned farmstead shelterbelts, windbreaks (agricultural shelterbelts), towns, potholes, pastures, and miscellaneous. When delineating habitats for uncolonized

stands, potholes were considered as habitat only if surrounded by shrubs or trees; no Common Grackle nest sites in cattail (*Typha* spp.) were observed during our two years of surveys in Benson County. Because of the continuous nature of vegetation distributions in towns, all nests in habitat classified as town were attributed to a single colony site.

County-wide habitat availabilities were estimated with the non-mapping technique (Marcum and Loftsgaarden 1980). We selected 200 quarters from our 1989–1990 surveys. Only quarters with vegetation capable of supporting Common Grackle nests were used. Five controls from each quarter were selected by placing an 80-grid, transparent sheet on an aerial photograph of the quarter and randomly selecting grids. Only colonizable habitats were selected, and non-nesting areas (e.g., croplands, roads, and water bodies) were not used.

We tested four null hypotheses: (1) DRS and DPW categories and vegetation were used as nest sites according to their availabilities in the colonies, (2) use of stands in colonized quarters was independent of both vegetation composition and DRS and DPW categories, (3) use of quarters was independent of vegetation and DRS and DPW categories, and (4) colony sites were distributed among the seven habitat categories in proportion to county-wide habitat availabilities. We used *G*-tests for goodness of fit to determine if actual use differed from expected (null) use for habitats, nest-site vegetation, and DRS and DPW categories in the colony sites (Sokal and Rolf 1981). If the *G*-tests were significant ($P \leq 0.05$), preference and avoidance were estimated using the Bonferroni method with an $\alpha = 0.05$ (Neu et al. 1974, Byers et al. 1984, Thomas and Taylor 1990). We used *G*-tests of independence to compare colony sites with uncolonized stands and to compare colonized and uncolonized quarters. Nest-site vegetation used <2% of the time was combined into a miscellaneous category. Vegetation height and DBH and DEG variables could not be transformed to approximate normality; therefore, Wilcoxon two-sample tests were used (Sokal and Rolf 1981). Pairwise comparisons of vegetation heights and DBH were made only for preferred and avoided species as determined by Bonferroni tests.

RESULTS

During our two-year study, we found 202 colonies with 3596 active nests on 177 of the 638 quarters surveyed. Thus, Common Grackles had a mean colony and nest density of 0.49 colonies and 8.81 nests per km^2 in Benson County, with 28% of the quarters occupied. In decreasing order, the most frequently used nesting substrates were blue spruce (N = 924), Siberian elm (N = 819), boxelder (N = 427), caragana (N = 238), and hawthorn (N = 230). Habitat classified as inhabited farmstead shelterbelt

TABLE 1

COMPARISONS[a] OF USE AND AVAILABILITY OF SEVEN HABITATS OCCUPIED BY 202 COMMON GRACKLE COLONIES IN BENSON COUNTY, NORTH DAKOTA, DURING 1989–90

Habitat	Availability (N = 1000) %	Use (N = 202) %	Preference[b]
Windbreak	25.6	24.3	0
Miscellaneous[c]	24.1	11.4	—
Pothole	22.7	6.9	—
Inhabited farmstead	10.9	32.2	+
Pasture	7.7	9.9	0
Abandoned farmstead	7.5	12.9	0
Town	1.5	2.5	0

[a] *G*-test for goodness of fit: G = 90.2, df = 6, $P < 0.0001$.

[b] "+" indicates preference, "—" avoidance, and "0" use according to availability. Preference was determined with Bonferroni confidence intervals ($\alpha = 0.05$) placed on use.

[c] Composition of the miscellaneous habitat category: lakesides (35%), woods (32%), roadsides (14%), ravines (14%), ditches (3%), and railroad easements (2%).

accounted for 57.8% of the nests. Towns, which occurred on five quarters, had the highest mean number of nests (N = 5, $\bar{x}$ = 142.5 nests/km^2, SE = 42.8).

Habitats were not colonized in proportion to their availabilities (G = 90.2, 6 df, $P < 0.0001$). Shelterbelts of inhabited farmsteads were used more frequently than expected, while potholes and miscellaneous habitats (e.g., woods, ravines, railroad easements, and lakesides) were used below expected frequencies (Table 1). Abandoned farmstead shelterbelts, pastures, towns, and windbreaks were used according to availabilities. Colonies were larger (Wilcoxon Two-sample Test: Z = 4.9, $P < 0.0001$) on quarters with inhabited farmsteads ($\bar{x}$ = 50.0 nests/km^2, SE = 5.5, N = 65) than on quarters with abandoned farmsteads ($\bar{x}$ = 14.4 nests/km^2, SE = 4.1, N = 26).

The use of quarters depended on plant species composition (G = 251.1, 18 df, $P < 0.0001$). Green ash, blue spruce, wild plum, and hawthorn occurred more frequently on colonized quarters (Table 2). Uncolonized quarters were typified by quaking aspen, plains cottonwood, and willow. We failed to detect differences between controls of colonized and uncolonized quarters for either vegetation heights or DBHs (all Ps > 0.05). Distance categories of controls differed between colonized and uncolonized quarters for farmsteads (G = 379.3, 3 df, $P < 0.0001$) and permanent water (G = 49.8, 3 df, $P < 0.0001$), with more controls on uncolonized quarters >500 m from both of these features.

Use of stands within colonized quarters was dependent on vegetation

TABLE 2

COMPARISONS[a] BETWEEN RANDOMLY SELECTED CONTROL VEGETATION (N = 5) FROM QUARTER SECTIONS COLONIZED BY COMMON GRACKLES AND UNUSED QUARTER SECTIONS

Vegetation	Uncolonized quarter sections (N = 350) %	Colonized quarter section[b] (N = 880) %	Preference[c]
Siberian elm (*Ulmus pumila*)	19.1	16.2	0
Blue spruce (*Picea pungens*)	0.0	3.8	+
Boxelder (*Acer negundo*)	8.6	11.9	0
Hawthorn (*Crataegus rotundifolia*)	1.4	4.2	+
Caragana (*Caragana arborescens*)	4.9	5.8	0
Green ash (*Fraxinus pennsylvanica*)	7.7	11.9	+
Chokecherry (*Prunus virginiana*)	6.9	8.4	0
Willow (*Salix* spp.)	21.4	12.5	—
Lilac (*Syringa vulgaris*)	1.1	1.9	0
Wild plum (*Prunus americana*)	0.3	3.0	+
Black poplar (*Populus nigra*)	0.0	1.0	0
Miscellaneous[d]	1.4	1.6	0
Bur oak (*Quercus macrocarpa*)	2.0	0.0	0
Honeysuckle (*Lonicera tatarica*)	0.6	1.5	0
Juneberry (*Amelanchier canadensis*)	0.6	0.8	0
American elm (*Ulmus americana*)	0.9	2.3	0
Aspen (*P. tremuloides*)	11.7	5.1	—
Russian olive (*Elaeagnus angustifolia*)	2.0	2.2	0
Cottonwood (*P. deltoides*)	9.4	5.9	—

[a] *G*-test of independence: $G = 251.1$, df = 18, $P < 0.0001$.

[b] One colonized quarter section consisted only of an abandoned shed surrounded by wheat and was not used in the analysis of vegetation.

[c] "+" indicates preference, "—" indicates avoidance, and "0" indicates use according to availability. Selection was determined with Bonferroni confidence intervals ($\alpha = 0.05$) placed on the vegetation from colonized quarter sections.

[d] Vegetation comprising <2% of the combined categories.

composition ($G = 252.4$, 17 df, $P < 0.0001$) (Table 3). Stands with Siberian elm, green ash, boxelder, caragana, hawthorn, blue spruce, lilac (*Syringa vulgaris*), and American elm (*Ulmus americana*) were more likely to be colonized than stands consisting of willow, plains cottonwood, and quaking aspen. Plains cottonwood had a larger DBH ($P = 0.04$) within colony sites ($\bar{x} = 39.0$ cm, SE = 4.2) than in uncolonized stands ($\bar{x} = 26.2$ cm, SE = 1.9). No differences in heights of control vegetation were detected between colony sites and uncolonized stands (all Ps > 0.05). The DRS categories were not independent between used and unused stands ($G = 221.4$, 3 df, $P < 0.0001$), with stands of vegetation in the 0–100 m and 101–300 m DRS categories colonized more frequently than stands in 301–500 and >500 m categories. The DPW categories between colony sites and unused stands were independent ($G = 4.7$, 3 df, $P = 0.192$).

TABLE 3

COMPARISON[a] WITHIN QUARTER SECTIONS USED BY NESTING COMMON GRACKLES BETWEEN RANDOMLY SELECTED CONTROLS (N = 5) FROM UNUSED STANDS OF VEGETATION AND COLONIZED STANDS

Species	Unused stands (N = 405) %	Colonized stands (N = 979) %	Preference[b]
Willow	33.6	8.0	—
Cottonwood	13.8	4.3	—
Siberian elm	11.8	17.7	+
Chokecherry	8.6	7.2	0
Aspen	6.2	4.0	—
Green ash	4.0	13.0	+
Boxelder	3.7	14.0	+
Wild plum	3.5	3.8	0
Caragana	3.0	7.0	+
Miscellaneous[c]	2.7	2.4	0
Russian olive	2.5	1.8	0
Hawthorn	2.2	4.8	+
Blue spruce	1.5	3.9	+
Honeysuckle	1.0	1.7	0
Black poplar	0.7	0.9	0
Juneberry	0.7	1.1	0
Lilac	0.2	2.1	+
American elm	0.2	2.2	+

[a] *G*-test of independence: $G = 252.4$, df = 17, $P < 0.0001$.

[b] "+" indicates preference, "—" indicates avoidance and "0" indicates use according to availability. Selection was determined with Bonferroni confidence intervals ($\alpha = 0.05$) placed on the vegetation from colonized stands.

[c] Miscellaneous category consisted of species that formed <2% of the combined categories.

Within colony sites, nesting vegetation was not used according to availability ($G = 203.6$, 17 df, $P < 0.0001$). Blue spruce, Siberian elm, and black poplar were used at greater than expected frequencies, whereas green ash, willow, American elm, quaking aspen, Russian olive, and plains cottonwood were used below expected frequencies (Table 4). The DRS categories were not used in proportion to their availabilities in colony sites ($G = 30.6$, 3 df, $P < 0.0001$). Nest sites ≤100 m from farmsteads were used more frequently than expected; all other DRS categories were used below expected frequencies. The DPW categories were not distributed randomly between controls and nest sites ($G = 8.8$, 3 df, $P = 0.032$); nest sites in the 301–500 m category were used more frequently, while nest sites >501 m from permanent water were used less frequently. Nest-site heights were greater than controls (all Ps ≤ 0.05) for Siberian elm, blue spruce, green ash, and American elm. The DBHs of nest sites were larger than controls for green ash and Siberian elm, while nest-site

TABLE 4

COMPARISONS[a] WITHIN COLONIES BETWEEN RANDOMLY SELECTED VEGETATION (N = 5) USED BY NESTING COMMON GRACKLES AND RANDOMLY SELECTED UNUSED VEGETATION

Species	Use (N = 799) %	Availability (N = 979) %	Preference[b]
Siberian elm	23.6	17.7	+
Blue spruce	15.5	3.9	+
Boxelder	11.9	14.0	0
Hawthorn	7.5	4.8	0
Caragana	7.5	7.0	0
Green ash	6.3	13.0	—
Chokecherry	5.4	7.2	0
Willow	4.8	8.0	—
Lilac	4.3	2.2	0
Wild plum	3.5	3.8	0
Black Poplar	2.8	0.9	+
Miscellaneous[c]	2.5	2.4	0
Honeysuckle	1.1	1.7	0
Juneberry	1.1	1.1	0
American elm	0.8	2.2	—
Aspen	0.8	4.0	—
Russian olive	0.6	1.8	—
Cottonwood	0.1	4.3	—

[a] *G*-test for goodness of fit: $G = 203.6$, df = 17, $P < 0.0001$.

[b] "+" indicates preference, "—" indicates avoidance and "0" indicates use according to availability. Selection was determined with Bonferroni confidence intervals ($\alpha = 0.05$) placed on use.

[c] Miscellaneous category consisted of substrates that formed <2% of the combined use and availability categories.

DBH was smaller for caragana. In 1990, nest sites were placed randomly with respect to DEG ($Z = 1.6$, $P = 0.12$).

DISCUSSION

Common Grackles prefer shelterbelts of inhabited farmsteads over six other habitat categories. Windbreaks, which offer structurally similar nesting substrates and are often adjacent to farmstead habitats, are used only according to availability. Windbreaks in North Dakota are usually single-rowed structures of Siberian elm and lack the areal extent and species heterogeneity of multi-rowed farmstead shelterbelts. Areal extent and species heterogeneity, however, can not account for the preference shown by Common Grackles for shelterbelts next to inhabited rather than abandoned farmsteads. Both classes of farmstead shelterbelts are of comparable size and species composition. Common Grackles may prefer shelterbelts of inhabited farmsteads because of the increased access to invertebrates. During the 1989 nesting season in Benson County, Common Grackles

used invertebrates as their major food (Homan et al. 1994). By establishing colonies near the maintained landscapes of active farmsteads, the birds may improve their foraging success for invertebrates (Yahner 1982). Anthropogenic supplementation of food and water resources (e.g., spilled grains, food, and water for livestock and pets) may further encourage Common Grackle colonization by inhabited farmsteads (Martin 1978: 141).

Habitat use was the broadest measurement of nesting distribution in our study. The vegetation and DRS data show that Common Grackles primarily nest by farmsteads. Excepting hawthorn, the vegetation characteristics associated with Common Grackle colonies were typical of plant species compositions found in multi-rowed farmstead shelterbelts. The use of pastures for colony sites probably cause hawthorn (and to a lesser extent wild plum) to be included with the shelterbelt vegetation. The apparent discrepancies among our vegetation analyses of Common Grackle colony and nest-site use were due to the scalar design of our study. For example green ash, which is avoided by Common Grackles within colony sites, is often planted in farmstead shelterbelts with more preferred nesting substrates (e.g., blue spruce); thus, green ash becomes an indicator of colonized quarters by association with preferred species.

In colony sites, Common Grackles apparently prefer blue spruce, Siberian elm, and black poplar over other plant species. These species are profusely branched, which aids in nest attachment; moreover, their dense foliage probably offers concealment and protection from excessive heat loss or gain. A warmer microclimate may allow for earlier initiation of egg laying (Erskine 1971). The foliage of Siberian elm and black poplar does not appear until May in northcentral North Dakota, and blue spruce (or other dense conifers) is the only nesting substrate favorable for initiating nests in April, the beginning of the breeding season in the state (Stewart 1975).

The rarity of blue spruce in habitats not classified as farmsteads made it impossible to directly separate the influence of human activity from the influence exerted by the structural characteristics of blue spruce. However, the combination of a preferred macrohabitat (inhabited farmstead) with a preferred microhabitat (blue spruce) may present the most favorable environment for nesting Common Grackles. The infrequent use of pothole habitat may have confounded the avoidance shown by nesting Common Grackles for structurally open vegetation, such as quaking aspen and plains cottonwood, but open-structured shelterbelt vegetation (e.g., green ash, American elm, and Russian olive) within colony sites was also used below expected frequencies. Our data support those of Yahner (1982) and Field (1971) who observed that green ash and other open shelterbelt plant

species were used infrequently or avoided by nesting Common Grackles. Avoidance is probably a result of the lack of secure nest attachments inherent in open-structured vegetation.

The presence of permanent water probably affects nesting behavior of Common Grackles. Similar observations concerning the association between Common Grackle colonies and water have been made (Erskine 1971, Bent 1958:398–399, Martin 1978:141). However, the birds may be responding to vegetation supported by water rather than to water itself (Erskine 1971). We located 14 colonies by potholes; although this habitat is avoided compared to availability, potholes may influence the association of colonies with permanent water.

Nesting substrate height may also be involved in nest-site selection, with Common Grackles displaying a preference for taller vegetation. Using taller vegetation allows for building nests at greater heights, which may provide for earlier detection of predators (Gutzwiller and Anderson 1987, Bekoff et al. 1987). Additionally, males often use taller vegetation for displaying (Petersen and Young 1950, Wiens 1965, Wiley 1976); these displaying sites may later become nest sites.

Planting more green ash and less blue spruce in farmstead shelterbelts may help reduce nesting densities of Common Grackles in this type of habitat. Structurally open vegetation, including open coniferous species such as ponderosa pine (*Pinus ponderosa*), probably deters nesting because of the lack of suitable attachments for nests. The planting of blue spruce windbreaks at distances >500 m from inhabited residences for reducing soil erosion should not encourage colonization.

ACKNOWLEDGMENTS

We thank D. Bergman, K. Fitzner, D. Foulk, K. Maier, C. Nelms, B. Osborne, K. Scheidecker and M. Soehren for their many hours of help in the field and lab. R. Dolbeer and G. Nuechterlein contributed valuable comments at the beginning of this study. D. Twedt assisted with the study design. We also thank landowners of Benson County for access to their properties. A. Barras, D. Bergman, D. Caccamise, R. Dolbeer, M. Kenyon, and an anonymous reviewer commented on earlier drafts of this manuscript. This research was supported by the Denver Wildlife Research Center, United States Dept. of Agriculture, Animal Plant Health Inspection Service, [Contract No. 12-34-41-0020(CA)] and the Dept. of Zoology, North Dakota State Univ., Fargo.

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EVIDENCE OF DUAL BREEDING RANGES FOR THE SEDGE WREN IN THE CENTRAL GREAT PLAINS

Paul A. Bedell

Abstract.—Sedge Wrens (*Cistothorus platensis*) are very rare breeders in the central plains states but show a pattern of mid-summer arrival dates. I examined their status in central Nebraska in August 1994 by conducting six Breeding Bird Survey routes and by searching suitable habitat. I recorded Sedge Wrens on three of the six survey routes. Most wrens occurred on sub-irrigated native meadows, but a variety of grassland types were used. Most clutches were initiated by the second week of August. Observers should be aware of the potential for late-summer breeding in other portions of their range. *Received 22 Mar. 1995, accepted 15 Aug. 1995.*

Although the breeding range of the Sedge Wren (*Cistothorus platensis*) includes much of the midwestern and northeastern United States (AOU 1983), it is apparently common and widespread only in the upper midwest, e.g., Minnesota (Janssen 1987) and Wisconsin (Robbins 1991). In much of the remainder of their breeding range in the United States, Sedge Wrens are rather rare, local, and erratic in occurrence. The breeding status of the Sedge Wren is an enigma as there are few or no nest records in many areas, combined with peculiar mid- to late-summer arrival dates. Such is the case in Alabama (Imhof 1962), Arkansas (James and Neal 1986), Kansas (Thompson and Ely 1992), Kentucky (Mengel 1965), Missouri (Robbins and Easterla 1992), Nebraska (Lingle and Bedell 1989), and Tennessee (Robinson 1990). McNair (1983) discussed summer occurrences of Sedge Wrens in the southeastern states and questioned whether these records indicate possible breeding activity. Late-summer breeding may occur in areas where wrens are absent in early summer, although nest records are very few. This phenomenon has been observed in Arkansas (Meanly 1952), Kansas (Schwilling 1982), and Nebraska (Lingle and Bedell 1989). Coincident with mid-summer arrival dates in more southerly areas is a "shifting about" in and out of nesting territories during mid-July in Minnesota (Burns 1982) and Illinois (Kroodsma and Verner 1978).

Sedge Wrens are highly opportunistic breeders that show little or no site fidelity (Walkinshaw 1935, Burns 1982), probably due to habitat instability (Kroodsma and Verner 1978). The ephemeral nature of wet grassland and marsh edge habitat dictates that species breeding in these habitats should be good dispersers (Remsen and Parker 1990). Some populations of Sedge Wrens are double-brooded (Burns 1982), and they are polygy-

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nous (Crawford 1977). Males build multiple nests which may be used for courtship activities, dormitories, or predator decoys (Burns 1982) and which are referred to in this study as dummy nests. One of these nests is lined and used by the female as a brood nest. However, nest building by males does not in itself prove breeding, as they may not attract a mate (Crawford 1977, McNair 1983).

In order to determine if territorial Sedge Wrens occurred in suitable habitat in late summer throughout central Nebraska, I censused selected Breeding Bird Survey (BBS) routes in August for the presence or absence of wrens. I also checked suitable habitat on a random basis in August and compared this to atlas data, nest records, and local ornithological literature. Clutch data came from this study and from field work which I conducted during the summers of 1988–1992 in Hall County, Nebraska.

METHODS

Previous field work in the Platte River valley indicated that in August Sedge Wrens often occur in the same type of wet meadows favored by Bobolinks (*Dolichonyx oryzivorus*). Therefore, I chose BBS routes based on relatively high numbers of that species. The chosen BBS routes had no previous records of Sedge Wrens. The mean numbers of Bobolinks per BBS route conducted from late May through mid-June from 1967–1992 were provided by the Breeding Bird Survey (B. Peterjohn, unpubl.). I also chose routes based on geographic coverage of central Nebraska and the Sandhills region. I conducted Nebraska BBS route numbers 007, 018, 026, 029, 041, and 116, between 8–14 Aug. 1994 and recorded the presence or absence of Sedge Wrens at half-mile intervals. I compared August Sedge Wren occurrence to June Bobolink occurrence at identical BBS survey stops with a Chi-square test (Ambrose and Ambrose 1987).

I also checked suitable habitat for the presence of Sedge Wrens throughout the central Nebraska area from 2–23 Aug. 1994 by stopping and listening from the roadside as I travelled. Several locations were reported by other observers. This area was bounded approximately by the Platte River valley, 102°W. Longitude in Cherry and Keith Counties, 98°W. Longitude in Hamilton County, and the South Dakota border. BBS routes were in Nebraska counties Buffalo, Cherry, Holt, Loup, and Wheeler. When access permitted, I searched for nests by first observing the birds, then by carefully pushing aside the vegetation as I walked through their territories.

I categorized wrens in a ranking of probable breeding evidence: (A) singing in suitable habitat, (B) nest building or dummy nests observed, (C) nest with eggs or adult feeding young. Because Sedge Wrens can build nests yet remain mateless, I considered breeding to be confirmed only when nests with eggs or offspring were observed or adults were observed carrying food. Clutch initiation was defined as the date the first egg was laid. Backdating a clutch to initiation was determined as one egg laid per day until clutch completion, thirteen days for incubation, and another fourteen days until fledging (Walkinshaw 1935, Burns 1982, pers. obs.).

Locations were marked on county maps and compared to Nebraska Breeding Bird Atlas data (Molhoff, unpubl.) and to June breeding records from state literature (Bruner et al. 1904, Cink 1973).

TABLE 1

NUMBERS OF SEDGE WRENS RECORDED ON BREEDING BIRD SURVEY (BBS) ROUTES IN NEBRASKA

BBS route number[a]	# Years run 1967–1992	Total June occurrences	August 1994
001	24	2	—
022	17	2	—
007	23	0	1
018	11	0	0
026	18	0	2
029	20	0	0
041	3	0	0
116	3	0	10

[a] Rows 001 and 022 are in northeastern Nebraska; routes 007, 018, 026, 029, 041, and 116 are in central Nebraska.

RESULTS

Three of the six BBS routes had Sedge Wrens singing on territories in August despite no previous June records. Only two BBS routes in Nebraska have ever reported Sedge Wrens, and then only rarely from the eastern border of the state. These records are from routes #001 in Otoe County, with individual reports in two out of 24 years, and #022 in Thurston County, also with individual reports in two out of 17 years (Table 1). I found no wrens in the central or western Sandhills region even though there appears to be much suitable habitat. Sedge Wrens occurred in this study only east of 100°W. longitude.

Even though the highest incidence of Bobolinks and Sedge Wrens occurred on the same route, there was no significant association between survey stops that recorded Bobolinks in June and identical stops that recorded wrens in August ($\chi^2 = 2.25$, df = 1, $P > 0.05$).

Seventeen additional sites with territorial Sedge Wrens were located in August 1994, mostly in sub-irrigated native meadows of the Platte River valley (Table 2). But one site was on Conservation Reserve Program (CRP) land idled for one season. Another site was on a three-year old dry 1.2 ha. native prairie planting. This prairie restoration site in Hamilton County, Nebraska, contained an active nest initiated on 9 August 1994.

Nine additional nests were discovered at Mormon Island Crane Meadows (MICM) in Hall County, Nebraska, in August 1989 and 1992. Two more nests in central Nebraska are described by Lingle and Bedell (1989) from August 1988. Most of these twelve clutches were initiated by the second week of August (Fig. 1). In addition, an adult wren with four

TABLE 2
HABITAT USE BY SEDGE WRENS IN NEBRASKA DURING AUGUST 1994

Habitat	Occurrences		
	Breeding evidence category		
	A	B	C
Subirrigated native meadow	6	3	1
Other wetlands	3	0	0
Prairie restoration and CRP land	2	0	1
Upland prairie	0	0	1

recently fledged young were reported from Buffalo County, Nebraska, in an upland prairie on 26 September 1994 (G. Lingle, pers. comm.).

DISCUSSION

Since Sedge Wrens can easily be overlooked, there is a possibility that they are present in these areas in early summer but delay the onset of breeding. This is unlikely due to the paucity of atlas, BBS, and other published records over many years. Stronger evidence of their early-summer absence comes from the Mormon Island Crane Meadows where ten

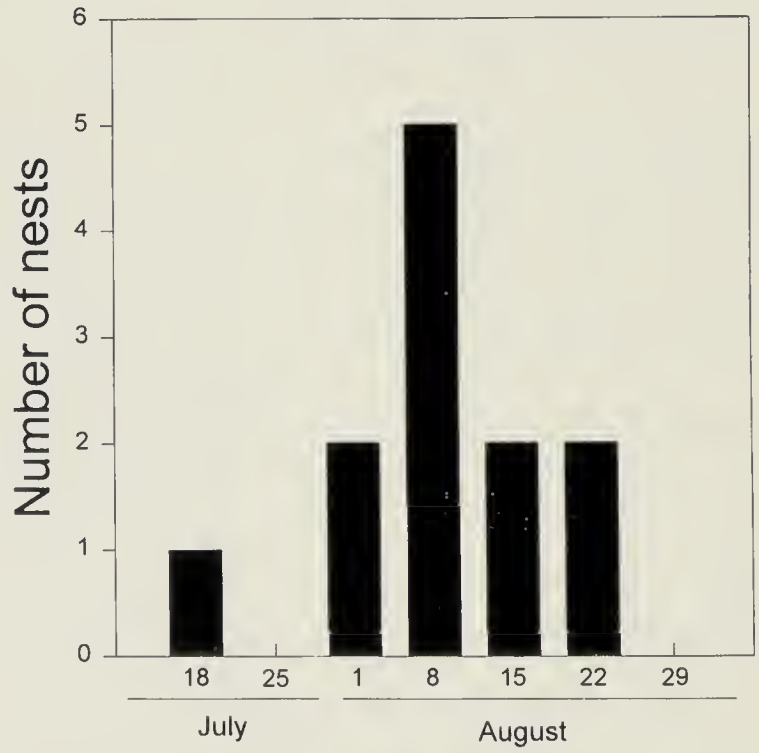

FIG. 1. Sedge Wren clutch initiation dates by week in Nebraska.

of the twelve active nests were located. Thirteen years of Breeding Bird Census studies conducted between 1980 and 1994 at MICM between 23 May and 20 June have recorded only single males in 1990 and 1994, and there are no records prior to June.

Although most wrens occurred on native wet grasslands, they showed a range of adaptability from partly flooded sites to dry prairie. The active nest in Hamilton County was on a dry level site devoid of any wetland vegetation. The adult with fledglings in Buffalo County was seen on a dry upland prairie. The Conservation Reserve Program (CRP) site was characterized by a rank growth of annuals up to 3 m in height. Sedge Wrens have also been recorded as using CRP lands in the Dakotas and Minnesota (Johnson and Schwartz 1993). Vegetative growth of at least 0.5 m was common to all sites.

The standard breeding phenology of most avian migrants includes a spring migration to a breeding region, establishment of a breeding site and raising offspring, and a return migration. The only North American migrant bird species known to possibly deviate from this pattern by utilizing dual breeding ranges is the Phainopepla (*Phainopepla nitens*) (Walsberg 1977). Phainopeplas breed in the Colorado Desert of California in March and April, then apparently migrate and renest in coastal oak woodlands from May through July. However, there is no direct evidence of this. The evidence for dual breeding ranges for Sedge Wrens is also conjectural in that there is no proof that they have first nested elsewhere before appearing in the central plains states in July and August. But the circumstantial evidence is compelling. The period of "shifting about" described by Burns (1982) and Kroodsma and Verner (1978) coincides with the arrival of Sedge Wrens in the central plains and in other states. The ephemeral habitat and low philopatry indicate a need and the ability for undertaking this highly unusual breeding strategy. The high mobility of Sedge Wrens may not be unique. There is an intriguing report of Yellow Rails (*Coturnicops noveboracensis*), which nest in similar habitat, nesting in late August in North Dakota (Lambeth 1994).

The breeding range of the Sedge Wren includes eastern Nebraska (Johnsgard 1979) and eastern Kansas (Thomson and Ely 1992), but this is based on very little actual evidence. A survey of historical early-summer breeding records from local ornithological literature, Nebraska Breeding Bird Atlas data (Molhoff, unpubl.), and the N.A. Nest Record program revealed only two June records of active nests in Nebraska (Bruner et al. 1904, Cink 1973). There are no June breeding records from Kansas and only two Kansas BBS routes, 020 in Barton County and 026 in Jefferson County, have reported Sedge Wrens, with a combined historical total of six birds. Schwilling (1982) described two active nests and recently

fledged young from Atchison County, Kansas, from August 1980. There is one North American nest record card of a probable dummy nest for Nebraska and none for Kansas. There are a handful of additional records of singing birds in appropriate habitat that possibly represent breeding activity (Cink 1973, Labedz 1984). Recently, July–August records in the Platte River valley of Hall County in central Nebraska indicate a regular mid-summer migration and nesting season in an area where they are largely absent until mid-July (Bedell 1987, Lingle and Bedell 1989). Observers have become aware of the influx of Sedge Wrens into the area in mid-summer where they have been recorded in numerous locations (Bedell 1987, Clausen 1989). A similar phenology has been noted for the Konza Prairie near Manhattan, Kansas (Zimmerman 1993). The breeding status of Sedge Wrens on the Konza Prairie has yet to be determined, where they occur annually in drainages that have ample stands of *Spartina.* When I visited the area on 25 Aug. 1994, I failed to find any activity, although wrens were present through at least 17 Aug. (J. Zimmerman, pers. comm.).

If Sedge Wrens have indeed first bred elsewhere in their range, then where are they coming from and why risk the hazards of migration? There seems to be little benefit for individuals that may have been successful in raising a first brood on a good territory to undertake the risks inherent in migration and of establishing another territory, so this migration should consist of individuals that accrue benefits in fitness that offset the costs. A possible explanation may be that because of the incidence of simultaneous polygyny (19% in Crawford 1977), bachelor males migrate to secondary areas such as the central plains anticipating a possible influx of females. If changing habitat conditions force Sedge Wrens to search for new territories in mid-season, these males would have an advantage, and the females would have an established territory to quickly move into. But if habitat conditions in the primary range remain favorable, few if any females may undertake this mid-summer migration. This may explain the lack of breeding evidence in some summers in Nebraska and elsewhere. Another good possibility is that they originate from the northern portion of their breeding range where a shorter season prevents them from raising a second brood. Or, perhaps these are individuals that occupied marginal territories which became unsuitable by July. This interesting problem certainly deserves further study.

If Sedge Wrens expand their breeding range into the central plains states in late summer, the same phenomenon should occur in other areas considered beyond their normal range. To understand the extent of this breeding range shift will require other observers to be aware of this possibility, and to take a closer look at the occurrence of late-summer Sedge

Wrens. This aspect of their breeding strategy needs to be determined for any understanding of the status of this possibly declining species.

ACKNOWLEDGMENT

This research was supported by the Margaret Morse Nice award of the Wilson Ornithological Society and the E. A. Bergstrom fund of the Association of Field Ornithologists. Bruce Peterjohn provided data and maps from the Breeding Bird Survey program. Gary Lingle of the Platte River Whooping Crane Habitat Maintenance Trust and Bill Whitney of the Prairie/Plains Resource Institute provided helpful information on field locations and permitted property access. Wayne Molhoff provided data gathered during the Nebraska Breeding Bird Atlas project. C. Blem, G. Lingle, and J. Zimmerman provided helpful comments on earlier versions of the manuscript.

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Wilson Bull., 108(1), 1996, pp. 123–128

DIETS OF NORTHERN PYGMY-OWLS AND NORTHERN SAW-WHET OWLS IN WEST-CENTRAL MONTANA

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Abstract.—One hundred ninety-four prey from 31 Northern Pygmy-Owls (*Glaucidium gnoma*) and 388 prey from 23 Northern Saw-whet Owls (*Aegolius acadicus*) were compared. Thirty-six percent of the pygmy-owl's prey was birds, whereas, 98.0% of the saw-whet owl's prey was small mammals, particularly voles. Food niche breadth and dietary evenness was 10.6 and 0.69 for pygmy-owls vs 3.3 and 0.89 for saw-whet Owls. Body mass of prey killed by both species was about 38 g. Dietary overlap between these two owl species was 37.0%, indicating that they fed on different prey assemblages. *Received 4 April 1995, accepted 28 Aug. 1995.*

Northern Pygmy-Owls (*Glaucidium gnoma*) and Northern Saw-whet Owls (*Aegolius acadicus*) overlap throughout much of their range in the western United States (AOU 1983). The natural history of Northern Pygmy-Owls is poorly known (Holt and Norton 1986, Holt et al. 1990), while that of Northern Saw-whet Owls is more certain (Cannings 1993).

In west-central Montana, Northern Pygmy-Owls and Northern Saw-whet Owls occur sympatrically from mixed deciduous and coniferous forested valley bottoms (975 m) to higher elevation (1584 m) coniferous forests (Holt and Hillis 1987). Both species are obligate cavity nesters, dependent upon woodpeckers or natural sites for nests. Both species forage similarly, using a perch and pounce technique. Northern Pygmy-Owls are crepuscular or diurnal, and Northern Saw-whet Owls are nocturnal. The diet of Northern Pygmy-Owls has been reported at the class level, while that of Northern Saw-whet Owls has been specific and thoroughly reviewed (Marks and Doremus 1988, Holt et al. 1991, Swengel and Swengel 1992). Several authors have compared the diets of sympatric owl's (Maser et al. 1970, Knight and Jackman 1984, Marks and Marti 1984, Nilsson 1984, Bosakowski and Smith 1992), but Herrera and Hiraldo (1976) in Europe, and Hayward and Garton (1988) in North America, have compared the diet of small cavity nesting forest owls. Herein, we compare their diet, prey biomass, food niche breadth (FNB), dietary evenness (DE), and dietary overlap (DO).

Pellets and pellet fragments from Northern Pygmy-Owls and Northern Saw-whet Owls were collected below roost trees near Missoula, Montana, during the non-breeding season—October through February 1987 to 1992. Pellets were dissected by hand, and prey species were identified

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and quantified using skulls and mandibles. Diurnal field observations of hunting Northern Pygmy-Owls with prey were also included. To evaluate these owls' trophic niches, we first compared prey species frequencies and percentages. We then computed the Shannon-Weaver diversity index to compare their FNB: where $H' = -\Sigma\ p_i \log p_i$ and p_i represents the proportion of each species in the prey sample (see Marti 1987). These values range from one to N, with larger values suggesting a broader food niche breadth. Dietary evenness was calculated using the equation; $F = (N_2 - 1)/(N_1 - 1)$, where N_1 is the antilog of the Shannon-Weaver index (H'), and N_2 is the reciprocal of Simpson's index (1/D) (Marti 1987). The dietary evenness values range from zero to one. As prey proportions become more equal, evenness values approach unity. To compare dietary overlap, we used the equation; $O = \Sigma\ p_{ij}p_{ik}/\sqrt{\Sigma\ p_{ij}^2\ \Sigma\ p_{ik}^2}$, where p_{ij} and p_{ik} are proportions of prey species in the diets of owls j and k, respectively (Marti 1987). The dietary overlap value ranges from zero to one, with zero meaning no dietary overlap and one meaning complete dietary overlap. We multiplied the values by 100 and report them as percentages for easier interpretation. Body mass of prey was set as the midpoint of the range. We did this because of inconsistencies with using the mean body mass from the literature, and age differences among prey species are not always delineated (Marti 1987, Holt et al. 1991, Holt 1993). Prey body mass data were taken from Dunning (1984) for birds and from Burt and Grossenheider (1976) for mammals. Prey was identified to species for the FNB, DE, and DO equations.

One hundred ninety-four prey items were recorded from 31 Northern Pygmy-Owls. Thirteen bird and four mammal species were eaten (see Table 1 for list and scientific names of prey items). Mammals represented 60.8% of the prey and birds at least 36.6%. *Microtus* voles represented 53.6% of the total prey eaten and 88.1% of the mammals eaten (Table 1). House Sparrows (*Passer domesticus*) represented 13.9% of the total prey eaten and 35.5% of the total birds eaten (Table 1). Food niche breadth was 10.6 (N = 99), and this value suggests a wide trophic niche. Dietary evenness was 0.69, which suggests that few prey species were evenly distributed in the diet. Prey body mass ranged from 3–167 g, $\bar{x}$ = 38.4 g.

Three hundred eighty-eight prey items were recorded from 23 Northern Saw-whet Owls. Six mammals and one bird species were eaten (see Table 2 for list and scientific names of prey items). Mammals represented at least 98.5% of the total prey, with deer mice, montane voles, and meadow voles, representing 92.0% (Table 2). When combined, *Microtus* species were more frequently eaten then *Peromyscus*, 57.9% vs 34.8%. Birds were numerically insignificant. Food niche breadth was 3.3 (N = 366)

TABLE 1
PREY SPECIES FROM 31 NORTHERN PYGMY-OWLS

Species	No.	%	MP	Range	Biomass (g)
BIRDS					
House Sparrow (*Passer domesticus*)	27	13.9	27	20–34	729
Pine Siskin (*Carduelis pinus*)	11	5.7	15	10–20	165
Evening Grosbeak (*Coccothraustes vespertinus*)	9	4.6	62	38–86	558
House Finch (*Carpodacus mexicanus*)	7	3.6	22	19–25	154
Dark-eyed Junco (*Junco hyemalis*)	5	2.6	20	14–26	100
Bohemian Waxwing (*Bombycilla garrulus*)	4	2.1	58	46–69	232
Northern Flicker (*Colaptes auratus*)	2	1.0	144	121–167	288
Black-capped Chickadee (*Parus atricapillus*)	2	1.0	11	8–13	22
Song Sparrow (*Melospiza melodia*)	2	1.0	20	11–29	40
Mountain Chickadee (*P. gambeli*)	1	tr.[a]	11	8–14	11
American Robin (*Turdus migratorius*)	1	tr.	83	63–103	83
American Goldfinch (*Carduelis tristis*)	1	tr.	14	8–20	14
Long-billed Marsh Wren (*Cistothorus palustris*)	1	tr.	11	9–13	11
Waxwing spp. (*Bombycilla* spp.)	1	tr.	—	—	—
Bird spp.	2	1.0	—	—	—
subtotal	76	36.6	—	8–167	2407
MAMMALS					
Vole spp. (*Microtus* spp.)	88	45.4	57	8–85	5016
Meadow Vole (*Microtus pennsylvanicus*)	13	6.7	49	28–70	637
Montane Vole (*M. montanus*)	3	1.5	57	28–85	171
Deer Mouse (*Peromyscus maniculatus*)	8	4.1	27	18–35	216
Vagrant Shrew (*Sorex vagrans*)	2	1.0	4	3–6	8
Mammal spp.	4	2.1	—	—	—
subtotal	118	60.8	—	3–85	6048
Total	194	100.0	—	3–167	8455

[a] tr. = trace amounts <1%.

suggesting a narrow trophic niche. Dietary evenness was 0.89, suggesting few species were eaten in similar proportions. Prey body mass ranged from 3 to 130 g, $\bar{x}$ = 37.7 g. Mean mammalian prey was 38.4 g.

Food niche breadth of the two species was strikingly different, with Northern Pygmy-Owls feeding on greater than three times as many species as Northern Saw-whet Owls (10.6 vs 3.3). Evenness values were also strikingly different (0.69 vs 0.89), and suggested that Northern Pygmy-Owls were not as restricted in their diet as Northern Saw-whet Owls. Thus, Northern Pygmy-Owls in our study area fed on a wider assemblage of prey than did Northern Saw-whet Owls. Dietary overlap was 37.0%, again indicating that these two species used different prey assemblages. At the generic level for mammals however, *Microtus* voles represented

TABLE 2
PREY OF 23 NORTHERN SAW-WHET OWLS

Species	No.	%	MP	Range	Biomass (g)
MAMMALS					
Deer Mouse (*Peromyscus maniculatus*)	134	34.5	27	18–35	3618
Montane Vole (*Microtus montanus*)	122	31.4	57	28–85	6954
Meadow Vole (*M. pennsylvanicus*)	101	26.0	49	28–70	4949
Vole spp. (*Microtus* spp.)	10	2.6	57	28–85	570
Shrew Spp. (*Sorex* spp.)	10	2.6	5	3–7	50
Vagrant Shrew (*S. vagrans*)	5	1.3	4	3–6	20
Masked Shrew (*S. cinereum*)	1	tr.	4	3–7	4
Northern Pocket Gopher (*Thymomas talpoides*)	2	tr.	104	78–130	208
subtotal	385	98.5	—	3–130	16,373
BIRDS					
Cedar Waxwing (*Bombycilla cedrorum*)	1	tr.	33	25–40	33
Bird Spp.	2	tr.	—	—	—
subtotal	3	tr.	—	—	—
Total	388	100.0	—	3–130	16,406

53.6% of the Northern Pygmy-Owl's diet and 60.1% of the Northern Saw-whet Owl's diet. This comparison suggests that *Microtus* voles were almost equally important to both species of owls.

Northern Pygmy Owls ate prey that averaged 38.4 g, with the smallest being a shrew spp. (4 g) and the largest a Northern Flicker (*Colaptes auratus*; 142 g). Northern Saw-whet Owls ate prey that averaged 37.7 g, with the smallest being a shrew (4 g) and the largest a northern pocket gopher (104 g). Yet the Northern Pygmy-Owl is the smaller of these two species. Indeed, average body mass for museum specimens of both species are Northern Pygmy-Owls: males 61.9 g, range 54–74 (N = 42) and females 73.0 g, range 64–87 (N = 10) and Northern Saw-whet Owls: males 74.9 g, range 54–96 (N = 27) and females 90.8 g, range 65–124 (N = 18) (Earhart and Johnson 1970), but also see Cannings (1993) for live weights.

This is the first quantitative review of the Northern Pygmy-Owls diet in North America and the first to compare its diet with another small sympatric forest owl. Previous authors (Holman 1926, Norton and Holt 1982, Holt and Norton 1986, Bull et al. 1987) have reported dietary data for Northern Pygmy-Owls. In these studies however, sample sizes were small (<35), and prey species were not always identified. An interesting similarity arises from these studies however. The percentages of birds in the Northern Pygmy-Owls diet were about 25 to 50% of the total prey,

26.0%, 32.0%, 47.0%, 36.0%, respectively. These data are similar to our results, and we know of no other North American owl species that shows such a preponderance of birds in its diet. During the breeding season however, Holman (1926) reported 42.0% lizards, and Norton and Holt (1982) and Bull et al. (1987) also reported 3.2% and 30.0% insects, respectively.

Diet of Northern Saw-whet Owls was consistent with other studies reporting their feeding ecology (Marks and Doremus 1988, Holt et al. 1991, Swengel and Swengel 1992). Prey body mass reported here (37.7 g) was in the upper limits of those reported by Cannings (1993). We believe this reflects the high proportions of *Microtus* voles in the owls diet from our study area.

Marks and Marti (1984) compared the trophic niche of breeding Long-eared Owls (*Asio otus*) and Barn Owls (*Tyto alba*). They concluded that competition could not be stated as shaping the owl's FNB. Hayward and Garton (1988) compared the diets of Boreal Owls (*Aegolius funereus*), Northern Saw-whet Owls, and Western Screech-Owls (*Otus kennicottii*). These owls ate similar sized prey, but sample sizes were too small for meaningful conclusions to be drawn. Bosakowski and Smith (1992) compared the trophic niche of Eastern Screech-Owls (*O. asio*), Barred Owls (*Strix varia*), and Great Horned Owls (*Bubo virginianus*) and concluded that the low dietary overlap was a result of size differences and habitat use between these owl species.

There is little conclusive proof about which mechanisms structure communities. Wiens (1989) listed two conditions that must be met for interspecific competition to exist (1) species must share resources, and (2) joint exploitation of those resources must negatively effect one or all species involved. We cannot conclude that diet is shaping the sympatric distribution of Northern Pygmy-Owls and Northern Saw-whet Owls in western Montana. Perhaps diel activity rhythms contribute to these owls' sympatry and reduced dietary overlap—Northern Pygmy-Owls are diurnal or crepuscular and Northern Saw-whet Owls are nocturnal. Prey activity rhythms may also influence spatial overlap between these species, and these type of data need to be incorporated into future studies of owl feeding ecology.

ACKNOWLEDGMENTS

We thank Charles Blem, Mike Maples, and Scott Swengel for comments on the manuscript.

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Wilson Bull., 108(1), 1996, pp. 129–136

EFFECTS OF EGG TYPE ON DEPREDATION OF ARTIFICIAL GROUND NESTS

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Abstract.—We examined depredation of artificial ground nests containing three egg types (brown chicken, white chicken, or Northern Bobwhite [*Colinus virginianus*]) in relation to plot age (clearcut vs uncut) and time period (trials 1–5) at the Barrens Grouse Habitat Management Area, Centre County, Pennsylvania, from May–July 1993. One hundred thirteen (38%) of the total nests were disturbed. Fewer nests were disturbed in clearcut (32%) than in uncut plots (43%) ($P \leq 0.05$). Clearcut plots had higher densities of brushy vegetation near ground level which better concealed nests and reduced foraging efficiency of predators. Rates of nest disturbance varied with time period ($P \leq 0.005$); in general, rates were greater in trials 1–3 than in trials 4–5, partially because of gypsy moth (*Lymantria dispar*) defoliation during trials 1–3. Nest fate also differed significantly ($P \leq 0.001$) with egg type. Rates of disturbance were lower with nests containing brown chicken eggs (24%) compared to nests containing white chicken eggs (46%) or Northern Bobwhite (43%) eggs. Nests with brown chicken eggs were better camoflaged and, hence, less likely to be disturbed. Based on our findings, we recommend that brown chicken eggs be used as an alternative to Japanese Quail (*Coturnix coturnix japonica*) eggs when simulating nests of Ruffed Grouse (*Bonasa umbellus*) or Wild Turkey (*Meleagris gallopavo*) in artificial ground nest studies. *Received 28 Feb. 1995, accepted 1 June 1995.*

The effects of egg size (e.g., Reistma et al. 1990) and egg color (e.g., Westmoreland and Best 1986, Yahner and DeLong 1992) have been examined in experimental studies designed to infer predation rates on nests of bird species with relatively small eggs. In addition, the effects of egg size on predation rates by American Crows (*Corvus brachyrhnchos*) have been investigated in meadows using large chicken eggs, small chicken eggs, and white painted Japanese Quail (*Coturnix coturnix japonica*) eggs (Montevecchi 1976). Relatively large eggs, including brown chicken, Japanese Quail, and Northern Bobwhite (*Colinus virginianus*) eggs also have been used in a variety of artificial nest studies as a means of determining rates of predation on nests simulating those of larger birds such as gallinaceous birds (e.g., Boag et al. 1984, Yahner and Wright 1985). However, no studies to our knowledge have examined differences in rates of nest disturbance on artificial ground nests in forested habitats using large eggs that differ in both size and color. This information is important in the experimental design of artificial nest studies intended to obtain estimates of predation on natural ground nests in various landscapes (e.g., Storaas 1988, Willebrand and Marcström 1988). Our objective was to compare rates of depredation among artificial ground nests containing

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three egg types that vary in both size and color and placed in forested plots of two age classes.

Study area and methods.—We conducted this study at the 1166-ha Barrens Grouse Habitat Management Area (HMA), State Game Lands 176, Centre County, Pennsylvania, the site of four previous studies of depredation of artificial ground nests (Yahner and Wright 1985, Yahner et al. 1989, 1993; Yahner and Mahan 1996). The Barrens Grouse HMA has been managed via forest clearcutting since 1976 by the Pennsylvania Game Commission to create habitat for Ruffed Grouse (*Bonasa umbellus*) (Yahner 1991, 1992). It contains an uncut (reference) and a cut (treated) sector of similar size. The treated sector is subdivided into 50% and 75% cut areas, corresponding to the amount of forest clearcutting and contained 136 contiguous, 4-ha blocks (e.g., see Yahner 1993, Yahner et al. 1993); 76 and 60 blocks are in the 50% and 75% areas, respectively. Each block is subdivided into four 1-ha (100 × 100 m) plots arranged in a checkerboard pattern (plots A–D). Our study was focused in the 75% area; in this area, plot A (western plot) in each block was clearcut during winter 1975–1976, and plot B (northern plot) was cut during winter 1980–1981, plot C (eastern plot) was cut in winters 1985–1986 or 1986–1987, and plot D (southern plot) was uncut.

Overstory trees (>7.5 cm dbh and >1.5 m tall) in plot D of the 75% area were about 70 years old and consisted primarily of quaking aspen (*Populus tremuloides*), bigtooth aspen (*P. grandidentata*), oak (*Quercus* spp.), and pitch pine (*Pinus rigida*). Common understory trees (2.5–7.7 cm dbh) and shrubs (<2.5 cm dbh) in all plots of the 75% area were aspen, dwarf chinkapin oak (*Q. prinoides*), scrub oak (*Q. ilicifolia*), and blueberry (*Vaccinium* spp.) (Yahner 1993).

Gallinaceous birds nesting at ground level at the Barrens Grouse HMA were Ruffed Grouse and Wild Turkey (*Meleagris gallopavo*) (Yahner et al. 1989, Yahner 1993). Potential predators on ground nests were American Crow, Blue Jay (*Cyanocitta cristata*), Virginia opossum (*Didelphis virginianus*), eastern chipmunk (*Tamias striatus*), gray squirrel (*Sciurus carolinensis*), red squirrel (*Tamiasciurus hudsonicus*), red fox (*Vulpes vulpes*), gray fox (*Urocyon cinereoargenteus*), black bear (*Ursus americanus*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), and weasel (*Mustela* spp.) (Therres 1982, Yahner et al. 1993).

We placed artificial ground nests during five time periods from late May to late July 1993 in the 75% area (Table 1). Each nest consisted of three fresh eggs put in a slight depression in leaf litter adjacent to a log, overstory tree, or stump (Yahner and Wright 1985, Yahner et al. 1993). Each nest contained one egg type: brown chicken, white chicken, or Northern Bobwhite. Based on a sample of 10 eggs/type, mean length and

TABLE 1

FATE OF 299 ARTIFICIAL GROUND NESTS IN RELATION TO AGE OF PLOT, TIME PERIOD, AND EGG TYPE AT THE BARRENS GROUSE HABITAT MANAGEMENT STUDY AREA, CENTRE COUNTY, PENNSYLVANIA, 1993

		Nest fate			
		Undisturbed		Disturbed	
Variable	Level	N	%	N	%
Age of plot	Clearcut	101	68	48	32
	Uncut	85	57	65	43
Time period	Trial 1	37	62	23	38
	Trial 2	35	58	25	42
	Trial 3	26	43	34	57
	Trial 4	46	77	14	23
	Trial 5	42	71	17	29
Egg type	Brown chicken	76	76	24	24
	White chicken	53	54	46	46
	Northern Bobwhite	57	57	43	43
Total		186	62	113	38

width of brown chicken eggs were 52 × 40 mm, white chicken eggs were 56 × 42 mm, and bobwhite eggs were 30 × 24 mm. Brown chicken eggs are light brown to buffy in color; white chicken and bobwhite eggs were dull or creamy white (Harrison 1975). Ruffed Grouse eggs were 39 × 30 mm (buffy), and Eastern Wild Turkey eggs are 63 × 45 mm (pale buff or buffy white) (Harrison 1975).

A trial was six days in length, with eight days between trials (methodology follows that of Yahner and Scott 1988). During each trial, 15 clearcut plots (plot C) and 15 uncut plots (plot D) were selected randomly. Two nests were placed in each plot; nests were separated by 30–35 m and placed 5 m from the edge of the plot. When placing nests, we wore rubber gloves and boots to minimize human scent at nests (Nol and Brooks 1982). This experimental design gave 60 nests/trial equally divided between the two plot ages and among the three egg types (total = 300 nests; one of the 300 nests was omitted from analysis due to incorrect placement).

We checked nests six days after placement between sunrise and 12:00 h (DST) to determine the fate (undisturbed, disturbed by avian predator, disturbed by unknown predator) of each nest (Yahner and Wright 1985). A disturbed nest was characterized by ≥ one broken or missing egg on day 6 of a given trial. Appearance and mode of disturbance of the eggs were used to identify predators as avian (e.g., peck hole in egg) or un-

known (Rearden 1951, Boag et al. 1984, Yahner and Wright 1985). In addition, eggs and eggshells were removed on day 6 of each trial.

We examined the dependency of nest fate (undisturbed vs disturbed) on plot age (clearcut vs uncut), time period (trials 1–5), egg type (brown chicken, white chicken, or Northern Bobwhite), using a four-way test-of-independence (Dixon 1990). Likelihood ratios (G^2) were used to test for interactions of nest fate with the three other variables, using log-linear models (Sokal and Rohlf 1981, Dixon 1990). Likelihood ratios are appropriate when analyzing attribute variables in multi-way contingency tables. If nest fate were significantly dependent on a given variable, we used *a posteriori* *G*-tests for goodness-of-fit about the cell (level) of interest (Sokal and Rohlf 1981). Because corvids are major predators on artificial nests at the Barrens Grouse HMA (e.g., Yahner and Wright 1985, but see Yahner et al. 1993), the frequency of nests disturbed by avian predators was compared among the three egg types using a *G*-test for goodness-of-fit.

RESULTS

One-hundred thirteen (38%) of 299 artificial ground nests were disturbed during the five trials (Table 1). Regardless of egg type, nest fate was associated with age of plot ($G = 4.7$, df = 1, $P < 0.05$). Fewer nests (all egg types combined) were disturbed in clearcut plots (N = 48, 32%) than in uncut plots (N = 65, 43%). Nest fate also was associated with time period ($G = 18.0$, df = 4, $P < 0.005$). The frequency of total disturbed nests in trial 3 (N = 34, 57%) was significantly higher than expected ($G = 6.3$, df = 1, $P < 0.025$), whereas frequency of total disturbed nests in trial 4 (N = 14, 23%) was significantly lower than expected ($G = 4.7$, df = 1, $P < 0.05$). In general, the percentage of disturbed nests/trial was greater in trials 1–3 (38–57%) compared to that in trials 4–5 (23–29%).

Nest fate varied with the three egg types ($G = 14.0$, df = 1, $P < 0.001$) (Table 1). The frequency of disturbed nests with brown chicken eggs (N = 24, 24%) was considerably lower than expected ($G = 8.2$, df = 1, $P < 0.005$), but the frequencies of disturbed nests with white chicken (N = 46, 46%) or Northern Bobwhite eggs (N = 43, 43%) were not different from expected (Gs ≤ 2.7, df = 1, $P > 0.10$). Moreover, there was a significant interaction among nest fate, egg type, and time period ($G = 17.9$, df = 8, $P < 0.05$). In particular, fewer nests with brown chicken eggs were disturbed in trial 1 (N = 2, 2%) than expected ($G = 6.0$, df = 1, $P < 0.05$), and more nests with Northern Bobwhite eggs were disturbed in trial 3 (N = 16, 14%) than expected ($G = 7.9$, df = 1, $P < 0.005$).

Thirty-six (32%) of the 113 disturbed nests were preyed upon by avian predators, principally Blue Jays and American Crows. The frequency of nests lost to avian predators differed among the three egg types (G = 11.9, df = 2, $P < 0.001$). Of the total nests disturbed by birds, eight (22%) were those containing brown chicken eggs, 22 (61%) had white chicken eggs, and six (17%) had Northern Bobwhite eggs. Avian predators destroyed more nests with white chicken eggs than expected (G = 11.6, df = 1, $P < 0.001$) and less with Northern Bobwhite eggs than expected (G = 5.1, df = 1, $P < 0.05$).

Discussion.—Our finding that rates of disturbance of artificial ground nests were lower in clearcut plots than in uncut plots concurs with results obtained in other studies of artificial nests at the Barrens Grouse HMA (e.g., Yahner and Wright 1985, Yahner and Cypher 1987, Yahner and Scott 1988). Clearcut plots were characterized by higher densities of brushy vegetation near ground level, which presumably better concealed artificial nests and reduced foraging of nest predators such as crows (Picozzi 1975) and raccoons (Bowman and Harris 1980). Moreover, uncut plots contained overstory trees that served as perch sites for avian nest predators (Yahner et al. 1989).

Most studies of artificial nests at the Barrens Grouse HMA have not documented significant differences in rates of nest disturbance over time (e.g., Yahner et al. 1989, 1993). However, as in the present study, Yahner and Wright (1985) found reduced rates of nest disturbance later in the breeding season, possibly because family groups of crows move to communal roosting sites and agricultural feeding sites (Cross 1946). Another possible explanation for greater nest disturbance in earlier trials of our study may be related to gypsy moth (*Lymantria dispar*) defoliation. Although we did not quantify the extent of defoliation caused by gypsy moth larvae, it was greatest during trial 3, which preceded the pupal stage of the life cycle and corresponded to the period of most extensive defoliation on the study area in spring and summer 1993 (Yahner and Mahan 1996). Extensive defoliation by gypsy moths has been shown to increase rates of artificial nest predation (Thurber et al. 1994).

Nests with brown chicken eggs in our study were better camouflaged and, hence, less likely to be disturbed by predators than other egg types, particularly by avian predators that rely on vision when foraging. A 24% disturbance of nests with brown chicken eggs was comparable to the rate found in a previous study at the Barrens Grouse HMA (Yahner et al. 1993). Our rate of disturbance of nests with Northern Bobwhite eggs (38%) was higher than that reported with an artificial nest study in Virginia using Northern Bobwhite eggs (20%) (Leimgruber et al. 1994).

In contrast to nests with brown chicken eggs, nests with more visually

conspicuous egg types, i.e., white chicken and Northern Bobwhite, were lost at a comparable rate despite appreciable differences in size between the two types. These results concur with those of Montevecchi (1976), who found similar rates of predation by American Crows on white eggs of three sizes placed in meadows. Perhaps because corvids are common nest predators at the Barrens Grouse HMA (Yahner and Wright 1985, Yahner and Scott 1988), color rather than egg size was the major factor influencing nest disturbance in our study. Although nests with Northern Bobwhite eggs were preyed upon as expected, conceivably many of the nests with missing Northern Bobwhite eggs at the end of trials could have been those in which eggs easily were carried away by large avian nest predators such as the American Crow (see Montevecchi 1976). For instance, of the 39 nests with no eggs present at the end of a given trial, the majority (N = 30, 77%) were those with eggs of Northern Bobwhite.

Some concern has been raised about size of eggs used in artificial nest studies (e.g., Boag et al. 1984, Reitsma et al. 1990, Roper 1992). Eggs of Japanese Quail used in artificial nest studies, for example, are considerably larger than those of songbirds, e.g., warblers, thereby potentially reducing rates of nest disturbance by smaller-sized mammalian predators that are less efficient at handling a larger egg (e.g., red squirrels and eastern chipmunks (Boag et al. 1984, Reistma et al. 1990). Thus, eggs used in our study, which were intended to simulate egg size of larger birds (e.g., Ruffed Grouse, Wild Turkey), probably were too large for handling by smaller predators.

Various investigators have often used either brown chicken eggs (e.g., Andren and Angelstam 1988, DeGraaf and Anglestam 1993, Yahner et al. 1993) or Japanese Quail eggs (Boag et al. 1984, Ratti and Reese 1988) as part of the experimental design of artificial nest studies in forested habitats. Based on our findings, we recommend brown chicken eggs as a suitable alternative to Japanese Quail eggs, both in terms of size and color, when simulating nests of Ruffed Grouse and Wild Turkeys in artificial ground nest studies.

ACKNOWLEDGMENTS

We thank J. R. Gillis, S. M. Partridge, and B. D. Ross for field assistance. This study was funded by the Pennsylvania Agricultural Experiment Station and the Max McGraw Wildlife Foundation.

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Wilson Bull., 108(1), 1996, pp. 137–150

FOOD AVAILABILITY AND FEEDING PREFERENCES OF BREEDING FULVOUS WHISTLING-DUCKS IN LOUISIANA RICEFIELDS

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ABSTRACT.—Expansion of the breeding distribution of the Fulvous whistling-duck (*Dendrocygna bicolor*) into the southeastern United States after the mid-1800s coincided with the establishment of rice (*Oryza sativa*) cultures in Texas, Louisiana, and Florida. In southern Louisiana, where approximately 80% of rice is aerially seeded in water, Fulvous whistling-ducks are suspected of feeding extensively on planted rice and are considered a nuisance. To determine the extent of rice utilization by ducks nesting in southwestern Louisiana, we estimated food availability in ricefields and assessed feeding preferences. We also examined effects of sex and stage of reproduction on food selection. Feeding sites in Louisiana ricefields that were tilled and flooded in preparation for spring planting, contained abundant foods (mean ± SE = 109.0 ± 18.0 g/m^2), especially seeds of moist soil plants such as signalgrass (*Brachiaria extensa*), beakrush (*Rhynchospora* sp.), and flatsedge (*Cyperus iria*). Diets of males and females were similar ($P = 0.080$), but varied through the reproductive cycle ($P = 0.008$). Consumption of plant material was slightly reduced during the period of rapid ovarian follicle growth in females; however, ingestion of animal foods never exceeded 4%. Fulvous whistling-ducks exhibited feeding preferences ($P < 0.001$) with aquatic earthworms (Oligochaeta) and wild millet seeds (*Echinochloa* sp.) being preferred over other food taxa. Rice made up <4% of the diet and was selected in proportion to its availability before and during period of rapid follicle development. Almost 25% of the diet of incubating females consisted of rice; however, we concluded that crop depredation by Fulvous whistling-ducks (≤0.1%) was of minor importance relative to other potential sources of crop loss. Indeed, use of ricefields by whistling-ducks may actually benefit farmers if ingestion of seeds of undesirable plants reduces the need for costly herbicide treatments. *Received 18 April 1995, accepted 22 Sept. 1995.*

Private lands provide critical habitat for many wildlife species, but wildlife use of these areas sometimes results in significant economic losses (e.g., crop depredation) or conflicts with intended land uses (e.g., designation as critical habitat for threatened or endangered species). Since 1987, >1 million ha of rice (*Oryza sativa*) have been planted annually in the United States, mostly in the Mississippi Alluvial Valley, Gulf Coastal Plain, and Central Valley of California. In these regions, ricefields similar to other seasonally flooded habitats receive high use by shorebirds, wading birds, and waterfowl (hereafter waterbirds). Rice prairies in eastern Texas, for example, provide wintering habitat for >2 million waterfowl (Hobaugh et al. 1989). In Louisiana and California, harvested ricefields

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are used extensively by feeding and resting waterbirds in winter and during fall migration (Miller 1987, Heitmeyer et al. 1989, Rave and Cordes 1993). Indeed, flooding of ricefields after harvest to provide wintering and migrational habitat for waterbirds has been actively promoted by some farmers' groups, agricultural extension services, state and federal wildlife agencies, representatives of the rice industry, and private conservation organizations. Advantages to rice farmers participating in winter flooding programs include enhanced waterfowl hunting (leasing) and viewing opportunities, as well as potential for positive public image, retention of nutrients and topsoil, weed control, stubble removal, and lowered tillage costs.

Ricefields may also receive high use by spring-migrating and nesting waterbirds (Helm et al. 1987, Hohman et al. 1994), but avian use of fields after they have been prepared for planting until harvest is actively discouraged. Waterbird use of ricefields in spring and summer may be especially great in areas such as southern Louisiana where most rice is planted in water ("water seeding"); that is, pregerminated seed is aerially dispersed over fields following discing, flooding, leveling or dragging with a blade, and settling of particulate matter. Water-seeded fields generally are drained within 24 hours of planting, but are reflooded from 7–14 days after rice has sprouted until 2–3 weeks before harvest. Elsewhere rice is mostly broadcast or drilled in dry fields ("dry seeding"). Both dry- and water-seeded fields may be flooded in winter and are managed similarly after rice has sprouted, so the principal difference between planting methods is the presence of water in fields immediately before spring planting. In spite of increased risks of seed depredation by waterbirds, water seeding is preferred by Louisiana rice farmers to control weeds.

Fulvous whistling-ducks (*Dendrocygna bicolor,* hereafter whistling-ducks) occur worldwide in tropical and semitropical regions (Johnsgard 1978). Their expansion into the southeastern United States in the late 1800s coincided with the establishment of rice cultures in Texas, Louisiana, and Florida (Lynch 1943, Bolen and Rylander 1983, Turnbull et al. 1989). The first breeding records for whistling-ducks in Louisiana were obtained in 1939 (Lynch 1943). Their numbers in Louisiana increased rapidly in the 1940s to perhaps 10,000 ducks but soon decreased because of hazing practices adopted by rice farmers to reduce crop depredation (McCartney 1963). Introduction of aldrin (a pesticide used to protect seed against larvae of rice water weevil [*Lissorhoptrus oryzophilus*]) in 1960, further depressed whistling-duck populations in Texas and Louisiana. Although the Louisiana population has recovered somewhat since 1970 when use of aldrin-treated seed was discontinued, numbers of whistling-ducks remain below peak counts observed in the 1940s in spite of in-

creased acreages of planted rice (Flickinger et al. 1977, Zwank et al. 1988).

Whistling-ducks nesting along the western Gulf Coastal Plain are migratory (Flickinger et al. 1973, Hohman and Richard 1994), arriving in southern Louisiana in February or March (McCartney 1963) when ricefields are being flooded in preparation for planting. Because of their presence in ricefields around the time of planting, occasionally in flocks of >2000 birds (Davis et al. 1944 in McCartney 1963), whistling-ducks are suspected of feeding on planted rice; consequently, they and, secondarily, other waterbirds (e.g., shorebirds and wading birds) are actively hazed from fields by rice farmers. We conducted this study to determine the extent of rice utilization by whistling-ducks nesting in southwestern Louisiana. Specifically, we estimated food availability in ricefields, assessed feeding preferences, and examined effects of sex and stage of reproduction on food selection by whistling-ducks.

METHODS

Whistling-ducks were collected on private agricultural lands in southwestern Louisiana, 9–15 May 1992 and 18 March–8 May 1993. Ducks were collected throughout the diurnal period and most were observed feeding for a minimum of 15 min before collection. Alcohol was injected into the gullets of specimens immediately after collection to minimize postmortem digestion of foods (Bailey and Titman 1984). We assigned pair status to birds on the basis of observations made before collection. Paired individuals were those showing active association, i.e., copulation, mutual display, female tolerance of the male or nonrandom spacing. Sex was assigned on the basis of cloacal characteristics (Hochbaum 1942). Specimens then were wrapped in paper towels and frozen in sealed plastic bags.

In the laboratory, thawed specimens were dissected and esophageal contents were removed, weighed (±0.01 g), and frozen. Carcasses were retained for contaminant analyses and proximate analyses of fat and protein composition. Ovaries removed from females were weighed (±0.01 g) and inspected for evidence of postovulatory follicles. We assigned females and their mates to the following reproductive categories, based in part on Krapu (1974): *Prenesting*—females with ovary mass ≤3 g and no post-ovulatory follicles; *Rapid follicle growth* (RFG)—preovulatory females with ovary mass >3 g and ovulating females; *Incubation*—birds collected at nest sites with embryo development ≥1 day (Weller 1956, Caldwell and Snart 1974).

Food availability was sampled at feeding sites by using a 6.1-cm diameter corer inserted to a substrate depth of at least 10 cm. Three or five core samples were taken at each feeding site. Corer contents (water column and substrate) were emptied into individual plastic bags and frozen. Thawed esophageal and core samples were hand-sorted to remove all macroscopic plant and animal material. Core samples were initially washed through a series of screens with 0.0625–4.0 mm^2 openings. Plant and animal taxa were separated, identified, and dried to constant mass (±0.001 g) at 50°C. Common names of invertebrates and plants followed Pennak (1989) and Scott and Wasser (1980), respectively. Food habits and availability were summarized on an aggregate percentage of dry mass basis (Swanson et al. 1974). Only food samples from birds containing ≥five items were included in the analysis (Reinecke and Owen 1980).

The proportion of plant material in the diet was compared by reproductive status and sex

using two-way analysis of variance with Type III sum of squares on arsine square-root transformed data (PROC GLM, SAS Institute, Inc. 1987). To determine if whistling duck diets differed between day and night, we compared occurrences (presence or absence) of rice in incubating birds collected before and after 08:00 h with a Chi-squared test (Conover 1980). Incubators collected before 08:00 h and found to have food in their esophagi were assumed to have fed at night. Food preferences were assessed on a dry mass basis by using PREFER, a computer program that assesses preferences using nonparametric procedures (Johnson 1980). Only foods having an aggregate percentage of dry mass ≥1 and ≥50% frequency of occurrence in use or availability samples were included in the analysis. These included foxtail (*Alopecurus carolinianus*), rice, junglerice barnyardgrass (*Echinochloa colonum*), broadleaf signalgrass (*Brachiaria extensa*), rice flatsedge (*Cyperus iria*), other flatsedges (*Cyperus* spp.), spikerush (*Eleocharis* sp.), beakrush (*Rhynchospora* sp.), razorsedge (*Scleria* sp.), mudplantain (*Heteranthera limosa*), buttercup (*Ranunculus* spp.), lesser swinecress (*Coronopus didymus*), morningglory (*Ipomoea* sp.), and aquatic earthworms (Oligochaeta). Aggregate percentages of dry mass of taxa collected at feeding sites were assumed to represent food available to whistling ducks at those sites. Significance level was set a priori at $\alpha = 0.05$.

RESULTS

Food availability.—Forty-nine cores were taken at 13 feeding sites in five southwestern Louisiana ricefields. Estimates of food density in individual ricefields ranged from 53.1–171.5 g/m^2 and averaged (± SE) 109.0 ± 18.0 g/m^2. Plant material consisted almost exclusively of seeds and made up >98 aggregate percentage of dry mass of available foods (Table 1). A minimum of 28 plant taxa were identified in availability samples of which only four taxa contributed >5%. Although animal foods made up <2% of available foods, they were present at all feeding sites. Only one animal taxon (aquatic earthworms) contributed appreciably to available foods.

Food use.—Eighty-five of 121 whistling-ducks collected in this study had ≥5 food items in their esophagi. Four males collected without mates were of unknown reproductive status and excluded from subsequent analyses. The proportion of plant material in the diet of breeding whistling ducks was similar in males and females ($F_{[1,75]} = 3.15$; $P = 0.080$) throughout the reproductive cycle ($F_{[2,75]} = 1.31$, $P = 0.276$), but varied among reproductive categories ($F_{[2,75]} = 5.21$, $P = 0.008$). Plant food consumption was somewhat reduced during RFG relative to other reproductive categories, but never decreased below 96% even in females. We found no difference in the prevalence of rice in esophagi of incubating whistling-ducks collected before and after 08:00 h ($\chi^2 = 0.024$, 1 df, $P = 0.84$). Plant foods eaten by whistling-ducks consisted almost exclusively of seeds from ≥29 taxa, 14 of which contributed ≥1% dry mass or occurred with ≥50% frequency (Table 2). Aquatic earthworms were the only animal food contributing appreciably to the diet.

Feeding preferences.—Whistling-ducks exhibited feeding preferences

TABLE 1
FOOD AVAILABILITY AT FULVOUS WHISTLING DUCK FEEDING SITES IN FIVE SOUTHWESTERN LOUISIANA RICEFIELDS

Food taxa[a]	Aggregate % dry mass	Percent occurrence	Dry mass (g/m^2)	
			Mean ± SE	Range
Plant	98.2	100.0	106.8 ± 17.2	52.6–165.4
Seeds	96.0	100.0	101.4 ± 16.5	52.6–165.4
Alopecurus carolinianus	2.3	100.0	1.5 ± 1.0	0.0–5.6
Oryza sativa	4.2	60.0	4.1 ± 2.1	0.0–12.6
Echinochloa colonum	1.2	100.0	1.0 ± 0.4	0.2–2.1
Brachiaria extensa	30.6	100.0	34.4 ± 9.2	2.4–60.7
Cyperus iria	10.7	80.0	8.9 ± 4.6	0.0–23.7
Cyperus spp.	2.3	100.0	2.3 ± 0.8	0.3–4.5
Eleocharis sp.	3.9	80.0	3.1 ± 2.2	0.0–12.9
Rhynchospora sp.	19.0	100.0	29.5 ± 16.3	0.0–96.6
Heteranthera limosa	6.9	100.0	3.1 ± 2.6	0.0–14.5
Ranunculus spp.	4.1	100.0	3.6 ± 1.5	0.6–9.7
Coronopus didymus	1.2	80.0	0.9 ± 0.6	0.0–3.3
Ipomoea sp.	1.2	80.0	1.1 ± 0.5	0.0–3.2
Miscellaneous[b]	8.4	100.0	8.0 ± 2.5	1.0–17.0
Other[c]	2.1	40.0	5.3 ± 4.7	0.0–26.4
Animal	1.8	100.0	2.2 ± 0.9	0.5–6.1
Oligochaeta	1.0	80.0	1.3 ± 0.9	0.0–5.5
Miscellaneous[d]	0.9	100.0	0.8 ± 0.2	0.5–1.6

[a] Includes only taxa with aggregate percentage of dry mass ≥1 and frequency of occurrence ≥50%.
[b] Miscellaneous seeds were from *Mollugo verticillata, Cerastium viscosum, Commelina* sp., *Eclipta* spp., *Serinea oppositifolia, Scleria* sp., *Fimbristylis miliacea, Sisyrinchium* sp., *Digitaria sanguinalis, Lolium temulentum, Panicum* spp., *Phalaris* sp., *Polygonum hydropiperoides, Polygonum portoricense, Solanum americanum,* and *Verbena* sp.
[c] Other plant material included unidentified roots and tubers.
[d] Miscellaneous animals included unidentified vertebrate and invertebrate eggs, Copepoda, Coleoptera (larvae and adults), Chironomidae (larvae and pupae), Corixidae (adults), Formicidae (adults), and Gastropoda.

during both the prenesting ($F_{[13,22]} = 36.60$, $P < 0.001$) and RFG periods ($F_{[12,16]} = 10.68$, $P < 0.001$). Aquatic earthworms and junglerice barnyardgrass were preferred over other food items during both reproductive periods (Table 3). Spikerush, flatsedge, and beakrush seeds were underrepresented in the diets, whereas rice was eaten in proportion to its abundance (Table 3).

DISCUSSION

Food availability.—Density of potential foods, especially seeds of moist soil plants, was high in Louisiana ricefields used by feeding whistling-ducks in spring. Our estimate of seed density at whistling-duck feeding sites (101.2 ± 16.5 g/m^2) was comparable to that (range, 90–134.4 g/m^2) in impoundments in the Mississippi Alluvial Valley managed spe-

TABLE 2

FOODS OF MALE (M) AND FEMALE (F) FULVOUS WHISTLING DUCKS COLLECTED IN AGRICULTURAL AREAS IN SOUTHWESTERN LOUISIANA

	Aggregate % dry mass			
	<RFG[a]	RFG		
	M+F	M	F	M+F
Food taxa[b]	N = 35	N = 15	N = 16	N = 31
Plant	98.1	99.0	96.1	97.5
Seeds	97.6	98.9	96.0	97.4
Lolium temulentum	0.0	0.6	3.4	2.0
Triticum aestivum	0.0	0.0	0.0	0.0
Phalaris sp.	tr[c]	0.2	0.3	0.2
Oryza sativa	3.6	1.4	6.1	3.8
Echinochloa colonum	8.9	9.3	13.3	11.3
Brachiaria extensa	27.8	49.3	45.2	47.2
Panicum spp.	0.3	tr	tr	tr
Cyperus iria	30.3	0.2	1.7	1.0
Cyperus spp.	0.2	1.4	0.8	1.1
Eleocharis sp.	0.6	0.0	0.3	0.2
Rhynchospora sp.	12.1	32.4	21.6	26.8
Scleria sp.	3.0	3.4	0.8	2.1
Heteranthera limosa	8.6	tr	tr	tr
Ranunculus spp.	1.1	0.2	0.5	0.4
Miscellaneous[d]	0.5	0.5	2.0	1.3
Other[e]	1.1	0.1	0.1	0.1
Animal	1.9	1.0	3.9	2.5
Oligochaeta	1.7	0.6	2.6	1.6
Miscellaneous[f]	0.2	0.4	1.3	0.9

[a] Reproductive categories: <RFG = prenesting females (and their mates) with ovary mass ≤3 g and no postovulatory follicles; RFG = preovulatory females with ovary mass >3 g and ovulating females; >RFG = birds collected at nest sites with embryo development ≥1 day.

[b] Includes only taxa with aggregate percentage of dry mass ≥1 or frequency of occurrence ≥50%.

[c] Trace (tr), aggregate % dry mass <0.1.

[d] Miscellaneous seeds were from *Coronopus didymus, Commelina* sp., *Eclipta alba, Eclipta* sp., *Serinea oppositifolia, Ipomoea* sp., *Cyperus compressus, Fimbristylis miliacea, Sisyrinchium* sp., *Alopecurus carolinianus, Digitaria sanguinalis, Phalaris* sp., *Triticum aestivum, Polygonum hydropiperoides,* and *Verbena* sp.

[e] Other plant material included unidentified roots, tubers, and other parts.

[f] Miscellaneous animals included unidentified invertebrate eggs, Coleoptera (larvae and adults), Chironomidae (larvae and pupae), Tabanidae (larvae), Formicidae (adults), and Mollusca (Gastropoda and Pelecypoda).

cifically for production of moist soil plants (Reid et al. 1989) and 2–4 times greater than densities of seeds and all other plant foods in nearby coastal marshes (Jemison and Chabreck 1962, Hohman et al. 1990, Bielefeld and Afton 1992, Manley et al. 1992). Observed seed densities were substantially greater than previous estimates obtained in Louisiana ricefields in late winter (4.3–38.0 g/m^2; Harmon et al. 1960, Davis et al. 1961); however, if selection of feeding sites by whistling-ducks was in-

TABLE 2
EXTENDED

% Occurrence					
>RFG	<RFG	RFG			>RFG
M+F	M+F	M	F	M+F	M+F
N = 15	N = 35	N = 15	N = 16	N = 31	N = 15
99.8	100.0	100.0	100.0	100.0	100.0
99.8	100.0	100.0	100.0	100.0	100.0
2.7	0.0	20.0	18.8	19.4	53.0
5.1	0.0	0.0	0.0	0.0	13.3
0.1	54.3	33.3	62.5	48.4	20.0
24.4	60.0	13.3	31.3	22.6	46.7
16.6	91.4	80.0	87.5	83.9	80.0
28.9	94.3	86.7	100.0	93.6	80.0
0.0	57.1	6.7	6.3	6.5	0.0
0.1	68.6	26.7	31.3	29.0	46.7
tr	45.7	46.7	18.8	32.3	13.3
tr	62.9	0.0	6.3	3.2	20.0
20.7	20.0	86.7	68.8	77.4	46.7
0.5	54.3	26.7	12.5	19.4	46.7
0.1	68.6	6.7	12.5	9.7	33.3
0.1	74.3	46.7	50.0	48.4	33.3
0.4	82.9	53.3	93.8	74.2	33.3
tr	28.6	26.7	18.8	22.6	6.7
0.2	68.6	60.0	100.0	80.7	26.7
0.1	51.4	46.7	68.8	58.1	13.3
0.1	40.0	60.0	93.8	77.4	26.7

fluenced by food availability (i.e., bird avoidance of sites with reduced food availability), then we likely overestimated food density in ricefields.

Abundance of potential foods in ricefields and their availability to feeding waterbirds vary temporally and geographically in relation to farming practices. Seed density in ricefield sediments is probably maximal immediately after autumn harvest (Harmon et al. 1960, Miller et al. 1989) and declines thereafter as a result of granivory, germination, physical degradation or destruction (e.g., tilling or burning), burial, and dispersal of seeds (McGinn and Glasgow 1963). To control noxious weeds such as red rice (*O. sativa* var.), most rice farmers in southern Louisiana practice a two-year planting cycle with rice cultivated in rotation with fallow, crayfish (Decapoda) aquaculture, pasture, or row crops (e.g., soybeans, milo, or wheat). Fields sampled in this study had been flooded and mechanically treated (disced and bladed) in preparation for water seeding of

TABLE 3

FEEDING PREFERENCES OF BREEDING FULVOUS WHISTLING DUCKS COLLECTED IN RICEFIELDS IN SOUTHWESTERN LOUISIANA

Reproductive status[a]	Preference rank[b]													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Prenesting N = 35	OLI[c]	ECH	SCL	COR	RHI	ORY	ALO	RAN	HET	BRA	IPO	ELE	CSP	CIR
Rapid follicle growth N = 28	ECH	OLI	RHI	HET	ORY	ALO	CIR	BRA	CSP	ELE	COR	IPO	RAN	

[a] Reproductive status: Prenesting = females (and their mates) with ovary mass ≤3 g and no postovulatory follicles; Rapid follicle growth = preovulatory females with ovary mass >3 g and ovulating females.

[b] Rank 1 = most preferred.

[c] OLI = Oligochaeta, ECH = *Echinochloa colonum*, SCL = *Scleria* sp., COR = *Coronopus didymus*, RHI = *Rhynchospora* sp., ORY = *Oryza sativa*, ALO = *Alopecurus carolinianus*, RAN = *Ranunculus* spp., HET = *Heteranthera limosa*. BRA = *Brachiaria extensa*. IPO = *Ipomoea* sp., ELE = *Eleocharis* sp., CSP = *Cyperus* spp., CIR = *Cyperus iria*. Foods underscored with the same line have statistically similar rankings ($P > 0.05$).

rice (i.e., rice had not been planted in these fields in the preceding growing season). Seeds found in our samples presumably were produced during the previous growing season. Thus, it is apparent that the farming practices implemented between rice plantings may have a large influence on seed abundance in Louisiana ricefields in spring. Outside of the Gulf Coastal Plain, rice is mostly dry-seeded with or without crop rotation. Flooding of ricefields, as is practiced by farmers that water-seed rice, is necessary for waterbirds to gain access to potential foods. The effect on food availability of mechanical treatments performed in flooded ricefields is unclear, but the appearance of large numbers of birds (shorebirds as well as waterfowl) in fields following such treatments, especially blading (W. L. Hohman, pers. obs.), suggests that food availability may be enhanced.

Feeding preferences.—Greater than 96% of the diet of male and female whistling-ducks nesting in southwestern Louisiana was composed of plant material. Animal foods were actively selected by whistling ducks before and during RFG (i.e., period of high protein demand in females), and animal food consumption increased slightly (females only) during RFG. Nonetheless, the amount of animal food eaten by whistling ducks during RFG was less than that reported for any other small-bodied waterfowl species (Krapu and Reinecke 1992: tables 1–5). Other female ducks, even those that are primarily herbivorous (e.g., Gadwall [*Anas strepera*], Ankney and Alisauskas 1991), substantially increase their consumption of animal foods to offset high protein costs of reproduction (Krapu and Reinecke 1992), but that apparently is not necessary for female whistling ducks. Black-bellied whistling-Ducks (*Dendrocygna autumnalis*) also eat only small amounts (<10%) of animal foods during the nesting period (Bourne 1981). Although the amount of animal material at whistling-duck feeding sites was low relative to plant material, our estimate of animal food density (2.2 ± 0.9 g/m^2) was comparable to that (2.65–2.87 g/m^2) found in freshwater coastal marshes where spring-migrating blue-winged teal (*A. discors*) consumed ≥56% animal material (Manley et al. 1992). This result suggests that whistling-ducks fed inefficiently on animal foods or that not all foods found in core samples were available to birds. It further suggests that proteins required for production of eggs must come from exogenous or endogenous sources in addition to those contained in animal foods eaten by birds during the daytime.

Whereas previous studies reported that whistling ducks using ricefields eat mostly rice (Imler 1944 in Meanley and Meanley 1959; Bruzual and Bruzual 1983), we found only limited consumption of rice by ducks nesting in southwestern Louisiana. Rice made up <4% of the diet and was selected in proportion to its abundance before and during RFG. Almost

25% of the diet of incubating whistling-ducks consisted of rice, but we were unable to assess feeding preferences of incubating whistling ducks because feeding sites were unknown and food availability therefore could not be determined. Whistling-ducks are known to feed in flooded ricefields at night (Meanley and Meanley 1959). The potential for crop depredation presumably is greatest at night when whistling-ducks can feed undisturbed. It is possible that our sampling of birds only during the daytime underestimated rice utilization by whistling-ducks; however, prevalence of rice in esophagi of incubating birds collected before 08:00 h (assumed to have fed at night) was similar to that of incubators collected after 08:00 h. Sample size used for this comparison was limited, but we interpret this result as evidence that bias associated with time of collection was minimal. We therefore concur with Meanley and Meanley (1959) that, relative to other seeds, rice was of minor importance in overall diet of whistling-ducks nesting in southwestern Louisiana.

Our conclusion that whistling-ducks ate small amounts of rice relative to seeds of other plants should not be interpreted as evidence that they caused no damage in ricefields. Based on energy requirements calculated for nesting whistling-ducks, we estimate maximum daily consumption of rice to be 44.5 g/bird or 44.5 kg/day for the entire population in southern Louisiana (Table 4). Thus, we determined the potential for crop depredation in southern Louisiana during the 60-day planting period to be ≤0.1% of seeded rice (Table 4). Previous estimates of crop loss caused by feeding whistling-ducks ranged from 0.25–2.0% (Imler 1944 in Meanley and Meanley 1959; McCartney 1963, Bourne and Osbourne 1978), but estimates made before 1965 probably do not accurately represent losses under current farming practices. Use of pregerminated seed, for example, greatly reduces the duration of flooding after planting and thereby limits availability of rice to feeding ducks. (We observed no diurnal feeding by whistling-ducks in dewatered fields.) Removal of water within 48 hours of planting also minimizes puddling or trampling of seeded rice (i.e., reduced sprouting caused by birds stepping on and burying rice seed; McCartney 1963). Concentrated feeding by large flocks of whistling-ducks may result in localized crop losses greater than those projected in this study, but we believe that such instances are uncommon. Under current farming practices, depredation is restricted to fields planted early in the growing season (before 1 April) when whistling ducks occur in flocks and temperatures are cool, requiring farmers to hold water on seeded fields >48 h. We further suggest that crop losses caused by whistling-ducks are of minor importance relative to other potential sources of crop loss such as other seed predators, variable seed germination rates, weather, and disease. Indeed, we suggest that use of ricefields by whistling-ducks

TABLE 4

ENERGY REQUIREMENTS OF BREEDING FULVOUS WHISTLING DUCKS AND POTENTIAL CROP LOSSES IN SOUTHERN LOUISIANA RICEFIELDS

Calculation assumptions	Sources
Total seeded rice in southern Louisiana = 22,662,080 kg	
Rice acreage = 202,340 ha	Anonymous (1995)
80% of acreage was water-seeded (i.e., available)	R. Levy (pers. comm.)
Seeding rate = 140 kg/ha	Anonymous (1995)
Maximum daily rice consumption/bird = 45.9 g	
Whistling Duck Diet = 100% rice[a]	
True metabolizable energy of rice = 3.34 kcal/g	Reinecke et al. (1989)
Body mass = 756 ± 4 g	W. L. Hohman (unpubl. data)
Basal Metabolic Rate (BMR) = 75 * (body mass [kg])$^{0.72}$	Owen and Reinecke (1979)
= 61.3 kcal/day	
Daily energy expenditures = 2.5 BMR	Owen and Reinecke (1979)
= 153.3 kcal/day	
Maximum seasonal rice consumption/population = 27,539 kg	
Planting season = 60 days	Anonymous (1995)
Population = 10,000 ducks	Flickinger et al. (1977)

[a] Actual range = 3.6–24.3% (This study).

may actually benefit farmers if ingestion of seeds of undesirable plants reduces the need for costly herbicide treatments.

ACKNOWLEDGMENTS

We thank the county agents in Acadia (R. Levy), Evangeline (A. Mire), and Vermillion (C. McCrory [deceased], H. Cormier, and M. Shirley) Parishes, and also F. Bowers (U.S. Fish and Wildlife Service) and C. Cordes (Southern Science Center) for their support of this study. We are sincerely grateful to the many rice farmers and other cooperators who shared information with us and/or granted us permission to conduct this study on their land. R. E. Olson and G. A. Weisbrich assisted in the field or laboratory. Helpful reviews of our manuscript were provided by S. Linscombe, Z. A. Malaeb, S. W. Manley, K. J. Reinecke, B. A. Vairin, and M. W. Weller. Collections were authorized under scientific permits issued to the senior author by the U.S. Fish and Wildlife Service (PRT-747267) and Louisiana Dept. of Wildlife and Fisheries (LNHP-93-02 and LNHP-94-21). Before implementation of this study, procedures involving use and care of birds were reviewed and approved by the Animal Use and Care Committee, Southern Science Center.

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Wilson Bull., 108(1), 1996, pp. 151–153

SHORT COMMUNICATIONS

Do standardized brood counts accurately measure productivity?—A standardized method for estimating raptor reproductive success and productivity is crucial for making valid comparisons among years and populations (Steenhof 1987). Steenhof and Kochert (1982) recommended that reproductive surveys be conducted when nestlings reach 80% of the average fledging age because nestlings are easily counted (Steenhof 1987), and little mortality occurs after this age and prior to fledging (Millsap 1981, Steenhof 1987). The utility of this recommendation would be enhanced if the number of nestlings reaching 80% of average fledging age was also indicative of a pair's productivity later in the nesting cycle. We tested this relationship in Prairie Falcons (*Falco mexicanus*) by measuring productivity at 80% of fledging age and at the end of parental care (approximately 35 days later or 27 days after fledging; McFadzen and Marzluff, unpubl. data). This latter measure of productivity was selected because attributes of habitat and land-use around nesting areas may affect productivity throughout the nesting period until parental care ceases and fledglings disperse.

In conjunction with a multi-year study of Prairie Falcon productivity (Lehman et al. 1993, Marzluff et al. 1993) in the Snake River Birds of Prey National Conservation Area in southwestern Idaho (area described in U.S.D.I. 1979), we knew the number of nestlings reaching 80% of fledging age and the number subsequently dispersing from the natal territory for 58 broods during the 1992 and 1993 breeding seasons. This sample included all sites we knew failed to produce fledglings (N = 24) and 34 sites where we radio-tagged nestlings (N = 141) and monitored their survival to dispersal (McFadzen and Marzluff, unpubl. data).

The number of nestlings attaining 80% of fledging age was significantly correlated with the number of young dispersing from a territory (Fig. 1; $r = 0.83$, $P < 0.001$, N = 58 broods), but the number of young per brood that survived to disperse differed substantially from the number of nestlings attaining 80% of fledging age. This difference was significant for broods of four (Paired $t = -3.2$, 11 df, $P = 0.008$) and broods of five to six (Paired $t = -3.9$, 16 df, $P = 0.001$) but not for broods of one to three (Paired $t = -1.6$, 4 df, $P = 0.18$). The relative inaccuracy of predicting the number of dispersers from the number of nestlings attaining 80% of fledging age was indicated by the large 95% confidence intervals associated with the mean difference between these two measures. The mean number of nestlings attaining 80% of fledging age was expected to be larger than the number of dispersers by up to 1.47, 3.91 and 4.37 nestlings, respectively for broods of three size classes (1–3, 4, and 5–6 nestlings; upper 95% confidence limits for difference between two means using one-sided confidence intervals; Hahn and Meeker 1991).

Variation in the number of young dispersing from broods of a given size required brood size to differ by at least two nestlings before significant differences in the numbers of dispersers were observed. The number of young dispersing from broods of one, two, or three (pooled $\bar{x} \pm$ SE = 1.2 ± 0.51, N = 5) did not differ significantly from the number dispersing from broods of four ($\bar{x} \pm$ SE = 2.7 ± 0.33, N = 12; Tukey's pairwise comparison, $P = 0.08$). The number dispersing from broods of four was not different from the number dispersing from broods of five or six (pooled $\bar{x} \pm$ SE = 3.5 ± 0.4, N = 17; Tukey's pairwise comparison $P = 0.20$). Broods of five or six produced more dispersers than broods of one, two, or three (Tukey's pairwise comparison, $P = 0.001$).

The significant correlation between the number of nestlings attaining 80% of fledging age and the number dispersing verifies that standardized nestling counts are indicative indices of a pair's productivity. However, we suggest that caution be applied in interpretations of

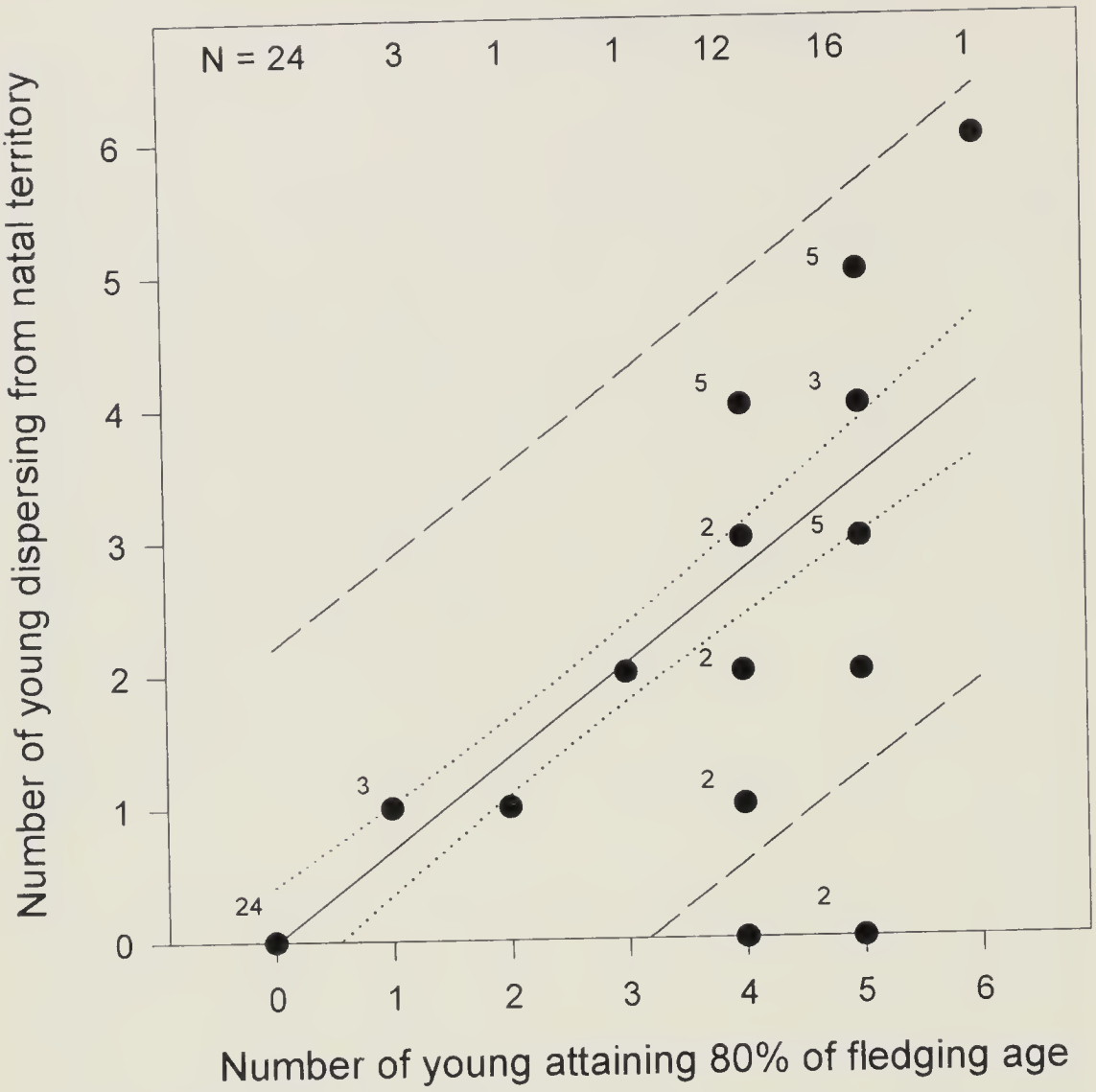

FIG. 1. Relationship between the number of young attaining 80% of fledging age (brood size) and the number surviving to disperse from the natal territory 35 days later. Sample sizes for each brood size are totalled at the top of the figure and listed next to each point with multiple observations. The least-squares regression line (solid line) and associated 95% confidence (dotted lines) and prediction intervals (dashed lines) are plotted.

brood counts as a measure of productivity for two reasons. First, brood counts may not accurately reflect the number of young fledging from the site. From 16% to 50% of young attaining 80% of fledging age died before they fledged (McFadzen and Marzluff, unpubl. data), and many more died before they dispersed (Fig. 1). Second, there was considerable variation in the number of dispersers produced from larger broods so that prediction intervals were large (Fig. 1) and brood counts needed to differ by at least two nestlings for differences to remain significant ($P < 0.05$) until the end of parental care. If a study compared a large number of broods between treatments (e.g., years, study areas, etc.), the resulting statistically powerful test could provide misleading conclusions about differences in productivity by showing that brood counts differing by less than two nestlings were significantly different ($P < 0.05$).

We support the use of standardized measures of productivity but urge researchers to measure productivity as late in the nesting cycle as possible. Measurements at earlier stages, such as Steenhof (1987) proposes, can be used to rank pairs in order of their productivity and to discriminate most successful pairs from failed ones. This may be adequate for studies designed to survey avian use of an area and to contrast the probability of successful reproduction among treatments. However, studies designed to compare brood counts among treatments, understand the demography of a population, or understand the factors that influence the reproductive success of individuals should not rely on measures of productivity made early in the nesting cycle because these are unlikely to correlate precisely with the number of young surviving to later stages.

Acknowledgments.—We thank the Raptor Research and Technical Assistance Center, National Biological Service, Boise, Idaho, for providing us with nesting data and field support. This note is a result of a cooperative research project between the U.S. Bureau of Land Management and the Idaho Army National Guard. Funding for the work was provided by the Idaho Army National Guard through the U.S. Army Chemical Research, Development, and Engineering Center to Greenfalk Consultants, contract # DAA 05-90-C-0135. M. Kochert, K. Steenhof, M. Vekasy, L. Schueck, D. Conner, and K. Beal provided helpful comments on earlier drafts of the manuscript.

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Wilson Bull., 108(1), 1996, pp. 154–159

Comparative foraging behavior of sympatric Snow Geese, Greater White-fronted Geese, and Canada Geese during the non-breeding season.—Interspecific comparisons of behavior provide a way to organize information for several species that can lead to hypotheses regarding the functional significance of observed interspecific differences (Clutton-Brock and Harvey 1984). Previous studies of goose time-activity budgets (e.g., Frederick and Klaas 1982, Giroux and Bédard 1990, Black et al. 1991, Ely 1992) have focused on single species and collectively were conducted under widely differing environmental conditions. Certain environmental factors are known to affect goose behavioral patterns and may confound direct interpretation of interspecific comparisons (Table 1). These environmental factors include geographic region, weather, presence of heterospecifics, group size, habitat and vegetation type, year, season, age, social status, and gender. We are aware of no studies that have controlled for environmental variation and examined differences in time-budgets solely as a function of species membership. The objective of this study was to identify interspecies differences (and similarities) in foraging behavior of geese during the non-breeding season, while accounting for sources of environmental variation.

Study area and methods.—This study was conducted from November 1991 to February 1992 and October 1992 to February 1993 southwest of Houston, Texas. The area, known as the rice-prairie region of Texas, lies inland from the coastal marshes and extends from Port Lavaca, Texas, eastward to the Louisiana border (Hobaugh et al. 1989, Gawlik 1994). We studied Snow Geese (*Chen caerulescens*), Greater White-fronted Geese (*Anser albifrons*), and Canada Geese (*Branta canadensis*; small races), the three most abundant species of geese wintering in the mid-continental United States (Haskins 1993). A fourth species, the Ross' Goose (*C. rossii*), also occurred in the study area but was much less common than the other three species (Harpole et al., in press).

We selected four groups of agricultural fields as sample sites, two each in Colorado and Wharton counties. Each site was approximately 2000 ha in size and contained the three most common types of ground cover (i.e., plowed soil, rice stubble, and annual plants) (Gawlik 1994). The sequence of visitation to sites was chosen randomly to reduce biases. Each site was observed from a vehicle driven along a pre-established route starting within one hour of sunrise, except when postponed by heavy rain, and ending by early to mid afternoon. Because we were interested in the foraging behavior of geese, we selected for behavior quantification only those flocks in which >50% of individuals were feeding. To reduce the chance of missing rare behavior or losing sight of individuals altogether, we selected only those flocks that provided reasonable visibility (<300 m). Flocks were characterized with regard to their species composition and relative abundances. After a 10-min settling period, flocks were filmed with a high-resolution 8-mm video camera and telephoto lens for about 15 min. Video tapes were later analyzed to construct 5–12 min continuous time budgets for one focal bird (Altmann 1974) of each species visible in mixed-species flocks and two focal birds of the same species for single-species flocks. If a focal bird became obscured during an observation period, the next closest individual of the same species exhibiting the same behavior was chosen to complete the focal sample. Behavioral categories included feeding stationary, feeding locomotion, non-feeding locomotion, resting (head pulled close to body or tucked under wing), comfort (preening and wing stretches), alert (head up), and aggression.

We quantified interspecies differences in the percentage of time spent on each behavior for each of the species-pairs (i.e., Snow and Greater White-fronted, Snow and Canada, and Greater White-fronted and Canada) with paired *t*-tests. We assessed individual variation in

TABLE 1

FACTORS AFFECTING TIME-ACTIVITY BUDGETS OF GEESE DURING THE NON-BREEDING SEASON

Study	Species	Source of variation[a]												
		Geographic region	Habitat or vegetation	Weather	Tide	Year	Season	Time of day	Group size	Presence of heterospecifics	Position within flock	Social status	Age	Gender
Frederick and Klaas 1982	Snow Goose		s	s, ns[b]		ns		s					s	ns
Ydenberg et al. 1983	Barnacle Goose (*Branta leucopsis*)			s					s					
Black and Owen 1988	Barnacle Goose					s	s	s						
Gauthier et al. 1988	Snow Goose	s	s	s	s			s						
Black and Owen 1989	Barnacle Goose						s						s	
Davis et al. 1989	Snow Goose		s			ns	s	s					s	
Turcotte and Bédard 1989	Snow Goose											s		
Giroux and Bédard 1990	Snow Goose	s				s	s							
Amat et al. 1991	Graylag Goose (*Anser anser*)		s											
Black et al. 1991	Barnacle Goose		s						s					
Bélanger and Bédard 1992	Snow Goose											s	s	ns
Black et al. 1992	Barnacle Goose										s, ns[c]			
Ely 1992	Greater White-fronted Goose	s	s	s		ns	s		s	s				
Schmutz 1994	Emperor Goose (*Chen canagica*)		s		s									

[a] s: statistically significant or used as a classification category; ns: statistically non-significant.
[b] Cloud cover was statistically significant, other weather variables were not.
[c] Some age and gender classes were statistically significant, others were not.

time budgets within a species by assigning members of single-species pairs randomly to one of two groups for subsequent analyses with paired *t*-tests as outlined above.

Because our sampling framework provided paired data on individuals foraging in the same location at the same time, we were able to control for sources of environmental variation, as identified in other studies (Table 1), such as geographic region, weather, presence of heterospecifics, group size, habitat and vegetation type, year, and season. We accounted for age differences by selecting only adults as focal birds for Snow Geese and Greater White-fronted Geese based on plumage differences. We could not, however, distinguish between adult and juvenile Canada Geese because both age classes have similar plumages. Gender was a potential source of variation we could not control because differences in body size or plumage were not discernable at the distances we viewed the geese. However, gender does not appear to influence significantly time-activity budgets of Snow Geese (Frederick and Klaas 1982, Bélanger and Bédard 1992) and we do not believe it had an effect on our analysis. Finally, our sampling scheme precluded our identifying social status of individuals. We assume that this potential source of variation was distributed randomly among the individuals we examined.

Results and discussion.—The Greater White-fronted Goose was the only species we observed in single-species flocks often enough to analyze the degree to which individual differences in behavior within a species affect time-activity budgets. Time spent on any behavior by Greater White-fronted Geese differed less than 2% among individuals (all tests, $df = 44$, $P > 0.05$). These data provide quantitative support for the notion that individuals of the same species within a flock behave similarly and thus are not completely independent (Gauthier et al. 1988, Giroux and Bédard 1990, Ely 1992). We suggest that individual differences within age and species classes are not a significant source of variation in time-activity budgets of wintering geese.

All three species spent most of their time feeding or in alert behavior, with substantially less time in other behavior (Fig. 1). The large amount of time spent feeding was not unexpected because we restricted our analysis to observations of flocks engaged primarily in feeding, and feeding has been reported as the primary activity for non-breeding geese in other areas (Gauthier et al. 1988, Bélanger and Bédard 1992, Ely 1992). Alert behavior is also a common activity in social birds, and indeed, most explanations of why birds forage in flocks are based on benefits from group feeding or antipredator behavior (Barnard and Thompson 1985). For many species of geese, the greatest cause of direct mortality is hunting (Boyd 1957, Owen 1980, Francis et al. 1992). In our study sites, hunting pressure was heavy and geese were frequently disturbed by nearby shooting; thus we viewed hunters as the main predator on geese. Another potential predator that frequently disturbed feeding geese was the Bald Eagle (*Haliaeetus leucocephalus*). This species is known to prey on geese in other areas (McWilliams et al. 1994) and it occurred regularly at our sites. However, during two years of study in which we recorded 122 eagle sightings, we observed only two attempts by eagles to capture living geese, and neither was successful. We observed coyotes (*Canis latrans*) in the same field with feeding geese only three times, out of 22 total coyote sightings, and they did not attempt to capture the geese.

Interspecific comparisons showed that time spent feeding differed among species by less that 11%, time spent resting differed by less than 8%, time spent alert differed by less than 4%, and other behavior collectively differed by less than 1%. None of these differences was statistically significant for Snow Geese and Greater White-fronted Geese (all tests, $df = 56$, $P > 0.05$) and Canada Geese differed only in the manner in which they fed (Fig. 1). Canada Geese spent more time in feeding locomotion than did Snow Geese ($df = 15$, $P = 0.007$) and Greater White-fronted Geese ($df = 28$, $P = 0.0001$) and less time feeding stationary than did Snow Geese ($df = 15$, $P = 0.059$) and Greater White-fronted Geese ($df = 28$, P

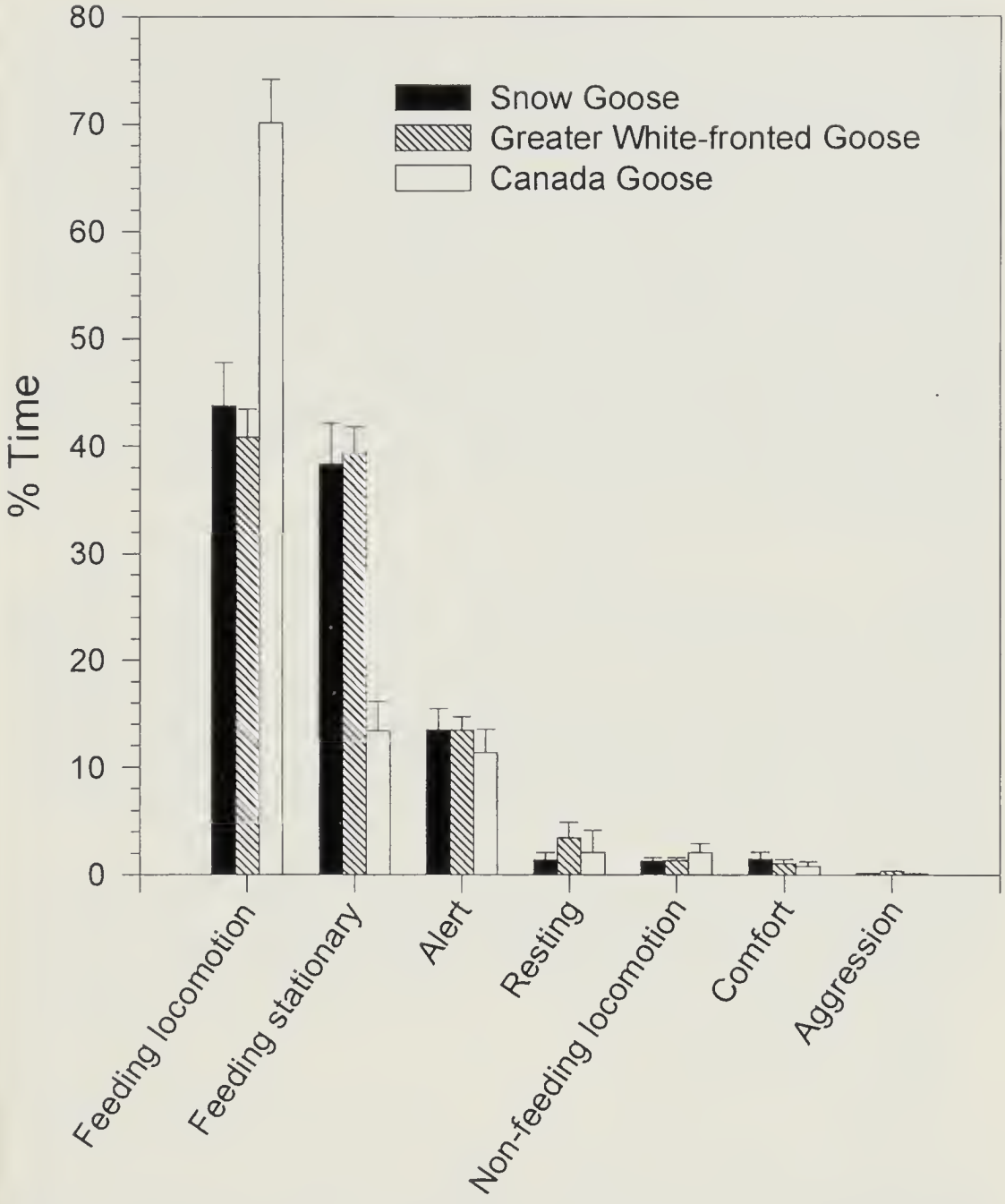

FIG. 1. Time spent on various aetivities by Snow Geese (N = 65), Greater White-fronted Geese (N = 122), and Canada Geese (N = 38) during the non-breeding season. Bars indieate the mean ±1 SE. Means represent pereentages pooled within a speeies using one foeal bird/species/floek.

= 0.004). These differenees in feeding behavior corresponded to differences in diet and morphology. Diet analysis of 16 geese eolleeted by DEG in fields of plowed soil and annual plants within the same study area, showed that subterranean portions of plants made up 27% and 17% of esophageal and proventrieuli eontents for Snow Geese and Greater White-fronted Geese respeetively, whereas Canada Geese eontained no subterranean material

(Gawlik 1994). White-fronted Geese and Snow Geese are larger than Canada Geese and more similar to each other in bill morphology. Overall, the smaller-bodied Canada Geese spent a greater proportion of their time walking and feeding on exposed portions of plants, whereas Snow Geese and Greater White-fronted Geese spent more time feeding in one location and consuming underground plant parts. Thus, although the type of feeding behavior exhibited by geese was related to morphology and diet, our results suggest that the overall time devoted to basic daily requirements such as consuming food and avoiding predation was similar for all members of a flock regardless of species.

Acknowledgments.—Funding for this study was provided by the Southeast Texas Wildlife Foundation, Texas Agricultural Experiment Station, and the U.S. Fish and Wildlife Service at Attwater's Prairie Chicken National Wildlife Refuge. DEG also received support in the form of a Tom Slick Graduate Fellowship. We acknowledge the many landowners who allowed us access to their property and provided additional insight into the wintering ecology of geese. We thank W. Hobaugh for his comments and suggestions during the study design. We also thank K. Bildstein, P. DuBowy, M. Clark, E. Klaas, and an anonymous reviewer for their comments on earlier drafts of this manuscript.

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Wilson Bull., 108(1), 1996, pp. 159–163

Survival of radio-collared nestling Puerto Rican Parrots.—A remnant population of the critically endangered Puerto Rican Parrot (*Amazona vittata*) survives in the Luquillo Mountains of northeastern Puerto Rico (Snyder et al. 1987). During the last three decades, intensive research and management have reversed a precipitous population decline to one of continual population growth (Wiley 1980, Snyder et al. 1987, Lindsey et al. 1989, Lindsey 1992). Prior to Hurricane Hugo in 1989, the wild population had grown from 14 birds during the mid-1970s to 47 (Meyers 1995). The hurricane reduced the population to about 22–24 birds; however, by early 1994, the population was estimated at 38–39 individuals (Meyers 1995). Population surveys for late 1994 (post-breeding) and early 1995 were 42 and 33, respectively (F. J. Vilella and F. Núñez, pers. comm.). These data invite optimism for the full recovery of the population because the species has shown the ability to recuperate about 83% of its pre-disturbance numbers within five years following a major disturbance.

Recovery of the species, however, will probably require relocation of wild parrots or releases of captive-reared parrots in the Luquillo Mountains and other suitable areas of Puerto Rico.

Low survival of free-flying, juvenile Puerto Rican Parrots hinders recovery efforts (Lindsey et al. 1994), and telemetry is the only reliable means for determining causes of mortality during this stage of the life cycle. Radio telemetry was first proposed in the mid-1980s as a field technique to monitor wild Puerto Rican Parrots. Using Hispaniolan Parrots (*A. ventralis*) as surrogates, S. A. Temple and E. Santana C. (pers. comm.) designed one of the first collar-mounted transmitters intended for future use on Puerto Rican Parrots. Early field research conducted by J. W. Wiley (Wiley 1983, Wiley et al. 1992) showed that radio telemetry was not only possible, but imperative, to determine survival rates of wild parrots. Until recently, telemetry was the only satisfactory method of individually identifying Puerto Rican Parrots in the field.

Herein, we report the resightings of three radio-collared Puerto Rican Parrots that were marked during 1985–1987 and present the expected survival for all radio-collared parrots released during those years. Our objectives are not only to report this information but to demonstrate that radio telemetry is crucial to our understanding of the Puerto Rican Parrot's ecology and indispensable for successful management and conservation.

Study area and methods.—The extant Puerto Rican Parrot population is confined to the 11,200 ha Luquillo Experimental Forest within the Luquillo Mountains and nearby forests (max. elev. ca 1000 m) of northeastern Puerto Rico (18°19′N, 65°45′W). Parrots nest among valleys and ridges at elevations of 370–670 m. Rainfall varies from 2000 mm in the foothills to more than 5000 mm on the highest peaks (Snyder et al. 1987). Following Holdridge's (1947) life zone classification scheme, the Luquillo Mountains are classified as subtropical wet and subtropical rain forest (Ewel and Whitmore 1973). More than 1200 plant species have been described, of which 240 are trees. Two forest types, tabonuco, characterized by its predominant species, tabonuco (*Dacryodes excelsa*), and palo colorado forest with the predominant palo colorado (*Cyrilla racemiflora*), constitute the dominant vegetative cover in the parrot nesting areas (Little and Wadsworth 1964, Snyder et al. 1987).

After relatively little disturbance in parrot areas for 50 years, major habitat disturbance was caused by Hurricane Hugo on 18 September 1989 which damaged much of the forest (Walker 1991, Walker et al. 1992). Although the parrot population declined 49%, presumably caused by the storm, the nesting population recovered within one to two years and produced six nesting pairs in 1991 and 1992 (Meyers et al. 1993).

From 1985 to 1987, 15 nestling parrots were radio-collared and released (Lindsey et al. 1994). In September 1985, three captive-reared parrots were released with radio transmitters (Snyder et al. 1987). Only one parrot survived the first week after the release. After 17 days, however, the sole survivor lost its radio 1.3 km from its release site. This parrot was identified by its leg band location in the spring of 1986. The second radio-marked parrot (No. 553) was hatched from a West Fork nest in 1986 and moved to an East Fork nest as a hatchling, a distance of about 1.3 km to the SSE. Parrot 553 successfully fledged on 25 June 1986 with a 6.3-g radio-collar attached (2.3% of its body weight). It was radio-tracked until 19 December 1986. The third parrot was one of the remaining 13 radio-collared and released from nests (wild-reared and foster captive-reared) on the eastern and western range of the Luquillo Mountains (Lindsey et al. 1994). All parrots were also marked with numbered stainless steel leg bands before release.

Results.—The first radio-collared parrot, released in 1985, was observed nesting at East Fork during 1989 and successfully produced one fertile egg that year (M. H. Wilson, pers. comm.). It was presumed dead after Hurricane Hugo when it failed to return to the nesting area with its mate.

During the 1991 breeding season, five years post-fledging, parrot 553 was observed with

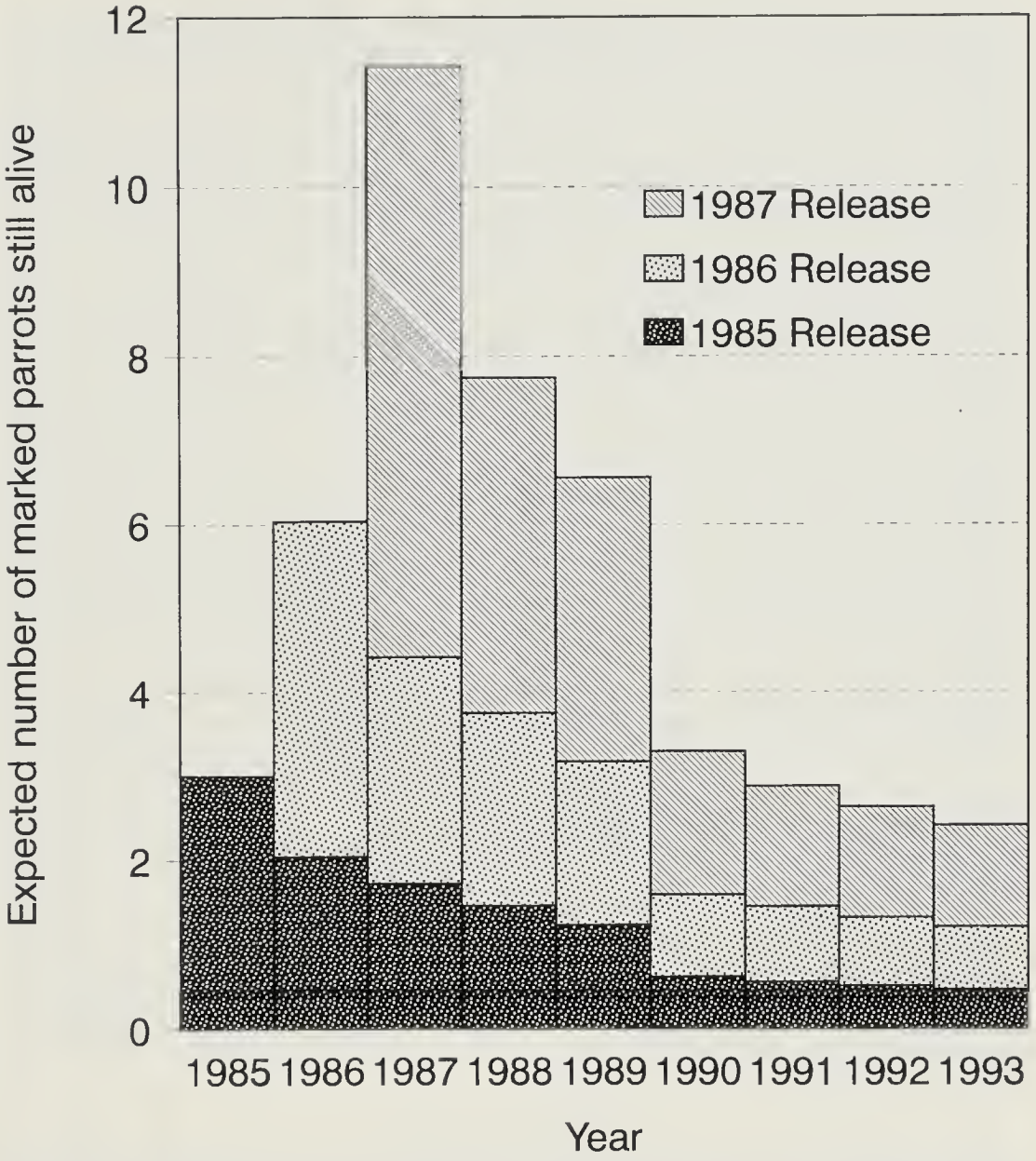

FIG. 1. Expected survival of marked Puerto Rican Parrots in the Luquillo Mountains, Puerto Rico, 1985–1987. Number of parrots radio-marked and released by year: 1985 = 3, 1986 = 4, 1987 = 7. Mortality estimated at 32.5% from fledging to one year of age, 15.2% for years 2–4, 8.7% per year after year 4 (Snyder et al. 1987, Lacy et al. 1989), and 50% (determined from surveys) for all parrots during the year of Hurricane Hugo. Survival for 1987 released parrots was ealculated from raw data for minimum number alive at six months after fledging.

its transmitter still intact at an East Mountain nest, 1.1 km NE of its natal site (B. Roberts, pers. comm.). It was the male of a breeding pair that suceessfully nested in a natural eavity of a tabonuco tree (Meyers et al. 1993). The parrot's identity was confirmed when its radio was shed inside the cavity during the breeding season and later diseovered during a nest check (H. Abréu, pers. eomm.). During the 1992 breeding season, this pair nested again in

the same cavity and produced fledglings (Meyers et al. 1993). By early 1993, parrot 553 had disappeared and was presumed dead when the female was seen with a new mate (B. Roberts, pers. comm.).

The third radio-collared parrot was sighted in the South Fork nesting area on 18 February 1993 by B. Roberts (pers. comm.). Roberts noted a large bulge in the parrot's neck feathers, attributing it to an unseen transmitter. Her observations were later verified by other observers when the parrot (with its radio still attached), replaced the male of the South Fork 1A nest-pair in early June of the same year.

Discussion.—Based on survival estimates for Puerto Rican Parrots (Snyder et al. 1987, Lacy et al. 1989) and assuming from previous experience no effect on survival due to the transmitter, we believe that two to three of the 15 parrots marked in 1985–1987 would be alive in 1993 (Fig. 1). Verifying that at least two of the radio-collared parrots were alive in that year demonstrates that this type of radio attachment may have little influence on juvenile survival. Another study of 15 parrots of four *Amazona* species in Puerto Rico during 1991–1993 resulted in no mortalities as a consequence of similarly designed radio-collars that remained attached for up to 1.8 years (Meyers, unpubl. data, Meyers 1995). One the 15 radio-collared parrots (female) and its unmarked mate successfully fledged two nestlings. We believe that important information gained by radio telemetry more than compensates for minor effects that this technique may have on the parrots. Because most parrots spend considerable time in groups, telemetry provides invaluable life-history and survival information.

Most of the radio-collared parrots probably lost their transmitters within 1–2 years. Radio attachments should be sufficiently secure to retain the transmitter for the predicted battery life. For two Puerto Rican Parrots in this study, however, the attachment material (heavy gauge cotton thread) had not deteriorated sufficiently to allow the successful shedding of the transmitter for almost four years after the battery had expired. Research is underway using a new radio-collar design and attachment mechanism to test the practicality of low carbon steel connectors that rust and allow the parrot to shed the collar after the battery expires (Meyers 1995).

Acknowledgments.—O. H. Pattee, J. H. Rappole, D. H. White, and J. W. Wiley provided helpful comments for improving the manuscript. The Puerto Rican Parrot Project is a cooperative program of the Puerto Rico Dept. of Natural and Environmental Resources; U.S. Dept. of Agriculture, Forest Service; and U.S. Dept. of Interior—Fish and Wildlife Service and National Biological Service.

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Wilson Bull., 108(1), 1996, pp. 164–166

New nesting area of Puerto Rican Parrots.—The Puerto Rican Parrot (*Amazona vittata*) population has been isolated in a 11,300-ha tract of the Luquillo Mountains of northeastern Puerto Rico for ca 80 years and has been using only a small area of the forest for nesting since the 1950s. During the last 50 years, it was known to have nested only in cavities of old growth palo colorado (*Cyrilla racemiflora*) with one exception (Snyder et al. 1987). In 1974, an occupied cavity was found in a laurel sabino (*Magnolia splendens*). Three to six nests have been monitored annually for the last 20 years, often in the same cavity trees for up to 11 years (Snyder et al. 1987, Meyers et al. 1993). The almost exclusive use of palo colorado trees for nesting has been caused by the scarcity of cavities in other tree species (Snyder et al. 1987). A recent study (Meyers and Barrow, unpubl. report) indicates, however, that potential palo colorado nesting trees have declined up to 72% since 1976 because of lack of natural recruitment. Only 7% of palo colorado stems were <30 cm diameter breast height (dbh), which indicates that further declines are expected in the future.

Snyder et al. (1987) conducted interviews that revealed that earlier in this century, the Puerto Rican Parrot occasionally nested in tabonuco (*Dacryodes excelsa*) and caimitillo (*Micropholis chrysophylloides*) cavities in the Luquillo Mountains. In northwestern Puerto Rico, Río Abajo residents reported that parrots commonly nested in corcho (*Pisonia subcordata*), aguacate (*Persea americana*), jácana (*Ponteria multiflora*), Puerto Rico royalpalm (*Roystonea borinquena*), and pot holes in limestone cliffs. Gundlach (1878, cited in Snyder et al. 1987) also reported that parrots nested in palms in the coastal plain near Quebradillas. Clearly, the Puerto Rican Parrot used a diversity of nesting sites in the past and might do so again in the future if nesting sites were available. I report here the habitat of a new nesting area of the Puerto Rican Parrot and suggest procedures that may encourage further expansion and changes in nesting habits of this critically endangered species.

Methods.—I located parrot activity sites during evening and morning surveys from a tree platform (20 m high) and by plotting the location of breeding pairs on maps with a compass and rangefinder. Habitat data were collected from 0.05-ha and 0.20-ha concentric, circular plots centered at the nesting tree (nesting site) and at activity sites of the pair in the nesting area. Data collected in the 0.05-ha plot were (1) elevation (m), (2) slope (%), (3) aspect (compass direction), (4) canopy height (m) measured by a rangefinder or Haga tree altimeter, and (5) vegetative strata. Midstory cover from 5-12 m high and canopy cover >12 m high were estimated by three persons using a scale of 1 to 4 (1 ≤ 25%, 2 = 26–50%, 3 = 51–75%, 4 ≥ 76%). Small trees, >2 m high and ≤30 cm dbh, were identified to species and counted. Large trees, >30 cm dbh, were identified to species and measured for dbh and height (m). Cavity openings were categorized by diameter classes: ≤5.0 cm, 5.1–20.0 cm, 20.1–35.0 cm, 35.1–50.0 cm, >50 cm. Potential parrot nest trees (>49 cm dbh, see Snyder et al. 1987) were tallied, identified as to species, and measured for dbh and height in 0.2-ha plots.

Results.—W. Abréu (O. Carrasquillo, pers. comm.) found the new nesting cavity in 1991. These parrots nested successfully and fledged young in 1991 and 1992 at East Mountain (Meyers et al. 1993), but the male was presumed dead in 1993 when its mate was seen at the cavity with another male (B. Roberts, pers. comm.). East Mountain is 1.1 km northeast of East Fork, a traditional parrot nesting area at higher elevations (500 m) in the palo colorado forest of the Luquillo Mountains. The newly discovered nesting cavity was in a 21-m high tabonuco tree (73 cm dbh) at an elevation of 370 m in tabonuco forest. Steep northwest slopes (55%) were prominent at the nesting site. Seven of eight trees >49 cm dbh and surrounding the cavity tree (0.2-ha plot) were potential nest trees. The nest cavity opening was 35–50 cm. Two smaller cavities openings (5–20 cm) were found in palo col-

orado trees nearby. Density of trees >30 cm dbh was 220 stems/ha, of which 35 stems were potential nest trees. Forest canopy and midstory cover in the area surrounding the nest tree was sparse to moderate (25–50% cover). At the nesting site, many colonizing trees (1640 stems/ha), such as trumpet-tree (*Cecropia sheberiana*), had recently sprouted (<6 cm dbh) after passage of Hurricane Hugo.

Habitat used by the breeding pair in the nesting area (activity sites, N = 3) was within 150 m of the nest and was oriented towards the northwest with slopes of 8–44%. Fewer potential nesting trees were found at these sites (12 fewer trees/ha). Density of trees >30 cm dbh was 100 stems/ha, of which 21 stems were potential nest trees. Forest canopy was broken and sparse (25–50% cover) at heights of 17.4–26.4 m. *Palicourea riparia* (626 stems/ha), *Psychotria berteriana* (373 stems/ha), and *Tetrazygia urbanii* (387 stems/ha), all small trees or shrubs (<6 cm dbh), were the predominant cover in the understory where few trumpet-trees were found (347 stems/ha).

Discussion.—These were the first Puerto Rican Parrots reported nesting in a natural cavity of a tabonuco tree since intensive research began in the 1950s (Rodríguez-Vidal 1959, Snyder et al. 1987). Old-growth tabonuco forest at East Mountain was selected for nesting by this pair in contrast with old growth palo colorado forest used in the past (Snyder et al. 1987, Meyers 1994). Few large trees (25 stems/ha >60 cm dbh) surrounded the nesting tree, which was considerably less than reported for the nearby East Fork nesting area (73 stems/ha >60 cm dbh) for palo colorado forest by Snyder et al. (1987) before Hurricane Hugo. The hurricane, however, reduced the number of potential nesting trees (>49 cm dbh) at East Fork to 23 stems/ha (Meyers and W. C. Barrow, Jr, unpubl. report). Preserving old-growth tabonuco forest in the Luquillo and other mountains of Puerto Rico may be important for the recovery of the species.

The high density of colonizers (e.g., trumpet-tree) at the nest site used by parrots at East Mountain was the consequence of extensive canopy openings caused by Hurricane Hugo. Parrot nesting areas at East Mountain and East Fork received significantly more hurricane damage than nesting areas on western slopes, where young trumpet-trees were almost nonexistent (0–20 stems/ha) in nesting plots (Meyers and Barrow, unpubl. report). This change in habitat, without the loss of large nest-trees, may have little effect on the parrot. Habitat damage, even from a severe storm, may not be detrimental to parrots and may actually stimulate the population growth rate (Meyers et al. 1993). To understand this effect, however, forest habitat simulation models may prove valuable in predicting potential effects of hurricanes and availability of potential nest-trees and food.

Although 47 cavities in palo colorado trees were enhanced for Puerto Rican Parrots in 1990, only one has been used in five years (E. García, pers. comm.). The site selection for enhancing cavities was based on parrot activity in the area which was determined by qualitative surveys. A recent study, however, revealed that parrot activity sites, based on quantitative surveys, are different from nesting sites for an important habitat characteristic. Nesting sites have 16–20 more potential nesting trees/ha than activity sites of parrots (Meyers and Barrow, unpubl. report). It may be beneficial to create clusters of cavities in potential nesting trees (palo colorado, tabonuco, caimitillo, and laurel sabino) in habitat similar to that used by the parrot for nesting, i.e. with a high density of potential nesting trees.

Acknowledgments.—Steven C. Latta, Eugene P. Odum, Paul W. Sykes, Jr., and two anonymous reviewers provided helpful comments for revising the manuscript. Wylie C. Barrow, Jr., Rafael de Leon, Jennifer D. Horn, and Keith L. Pardieck collected parrot activity and habitat data. The Puerto Rican Parrot Project is a cooperative program of the Puerto Rico Dept. of Natural and Environmental Resources; U.S. Dept. of Agriculture, Forest Service; and U.S. Dept. of Interior—Fish and Wildlife Service and National Biological Service.

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Wilson Bull., 108(1), 1996, pp. 166–170

Neotropical migrants in marginal habitats on a Guatemalan cattle ranch.—Recent studies of migratory birds overwintering in Central America and the Caribbean have focused on bird communities in particular types of disturbed habitats, such as citrus orchards (Rogers et al. 1982, Mills and Rogers 1992) or agricultural fields in varying stages of succession after human abandonment (Waide 1980, Kricher and Davis 1989), while others have attempted to discern broader patterns of species occurrence across a wide variety of habitat types (Waide et al. 1980, Leck 1985, Lynch 1989, Robbins et al. 1992, Wunderle and Waide 1995). Although a few in the latter category have included a small amount of data from cattle ranches, Central American cattle ranches have received little attention in the ornithological literature. This is unfortunate because conversion to cattle ranching is the single largest threat to the remaining undisturbed lands in Central America (Myers 1980, Buschbacher 1986, Lynch 1989). Given the amount of land already used for cattle ranching in Central America and the amount likely to be converted in the near future, knowledge of patterns of species occurrence on land modified for cattle ranching is critical for formulating future conservation strategies.

We mist netted birds on an active cattle ranch in the Pacific lowlands of Guatemala to investigate the extent to which narrow riparian corridors and other marginal habitat set in a matrix of open cattle pasture serve as usable habitat for overwintering migratory birds.

Study area and methods.—We conducted the study from 2 February to 2 March 1995 on Finca Caobanal, a working cattle ranch in the Pacific lowlands of Guatemala. The region is characterized by relatively flat topography with elevation ranging from sea level to approximately 200 m. The average annual temperature is 25°C, and annual rainfall averages 200 cm, with a pronounced dry season between November and April (Universidad Rafael Landívar 1987). Although the native vegetation type is subtropical humid forest, the vast majority of the region has been converted to agricultural land, particularly cattle pasture, and more recently, sugar cane.

Finca Caobanal comprises approximately 1000 ha situated along the Maria Linda River, about 30 km southeast of the town of Escuintla. The ranch is a mosaic of open pastures separated by hedgerows and artificial canals lined with narrow corridors of secondary growth vegetation and one 250-ha parcel of secondary growth forest. The riparian corridors range in width from approximately 10–80 m; lower and mid-story vegetation is generally dense and is dominated by tall grasses, *Heliconia* sp., *Acacia hindsii, Ricinus communis* and *Piper* sp. Isolated overstory trees include *Pithecolobium saman, Bombax ellipticum, Acacia hindsii, Enterolobium cyclocarpum, Salix* sp. and *Ficus* sp. In the secondary growth forest, dominant tree species include *Terminalia oblonga, Cedrela odorata, Ficus* sp., *Triplaris malaenodedron* and *Cecropia* sp., and the average canopy height is 15–20 m. The understory is relatively open, but in some places is dominated by large patches of *Heliconia* sp.

Although previous studies that surveyed avian communities on cattle ranches in Central America (Saab and Petit 1994, Robbins et al. 1992, Lynch 1989) focused on open pasture, deliberately avoiding edges and hedgerows, we focused our mist netting efforts in the vegetation on the margins of actively grazed cattle pastures, in the riparian corridors along the irrigation canals, and in the 250 hectare forest. Two to seven black nylon 30 mm mesh nets (depending on habitat shape and size) were operated daily, generally in a line with approximately 12m between each net, and one or two nets situated perpendicular to the others. In order to avoid heat stress on the birds, nets were checked every 15 min and were closed between approximately 10:30 and 15:00. Nets were moved every three days to lessen the problem of net shyness and were open for a total of 446 net-h. Birds were marked with indelible ink underneath the wing in order to identify recaptures.

Mist netting is strongly biased against species that spend most or all of their time in the canopy, and this investigation should therefore be viewed as a study of primarily understory birds. Additionally, using mist net data to infer absolute species abundance directly is problematic because some species have a higher probability of capture than others; nonetheless, when interpreted cautiously such data can still serve as a meaningful index of relative species abundance (Karr 1981).

Results.—We caught 258 individual birds of 45 different species; 49% of individual birds were long-distance migrants, and 51% were residents (Table 1). This approximately 1:1 ratio of overwintering migrants to residents is consistent with other published netting studies conducted in secondary growth habitats in Central America and the Caribbean (Lynch 1989, Waide 1980).

The five migratory songbird species most frequently captured were Yellow Warbler, *Dendroica petechia* (N = 22), Common Yellowthroat, *Geothlypis trichas* (N = 16), Northern Waterthrush, *Seiurus noveboracensis* (N = 10), Yellow-breasted Chat, *Icteria virens* (N = 8), and Painted Bunting, *Passerina ciris* (N = 15). The first four species are widely reported to be abundant on disturbed and/or agricultural lands in Central America (Rogers et al. 1982, Kricher and Davis 1992, Petit et al. 1992, Robbins et al. 1992, Lynch 1992, Mills and Rogers 1992), but the Painted Bunting is less well-documented as an inhabitant of severely human-modified environments in Central America.

Capture rates of birds in the riparian corridors were strikingly different from those in the secondary growth forest; working in the corridors we caught an average of 76 birds per 100 net-h, compared to only 20 birds per 100 net-h in the forest ($\chi^2 = 30.5$, $P < 0.01$). The low capture rate in the forest may have resulted partly from the fact that the average forest canopy height was considerably greater than in the corridors, and consequently canopy-foraging birds may never have flown low enough in the forest to be captured. We do not believe this entirely explains the disparity, however, as casual observations also indicated a greater density of birds in the riparian corridors. Although casual observations may have been biased by a lower probability of detection of birds in the forest canopy, the corrobo-

Table 1

Bird Species Netted at Finca Caobanal

Species	Number captured	Migratory status
Ruddy Ground-Dove (*Columbina talpacoti*)	3	R
Common Ground-Dove (*C. passerina*)	1	R
Groove-billed Ani (*Crotophaga sulcirostris*)	1	R
Cinnamon Hummingbird (*Amazila rutila*)	28	R
Ruby-throated Hummingbird (*Archilochus colubris*)	1	M
Amazon Kingfisher (*Cholorceryle amazona*)	1	R
Smoky-brown Woodpecker (*Venilornis fumigatus*)	1	R
Ivory-billed Woodcreeper (*Xiphorynchus flavigaster*)	2	R
Barred Antshrike (*Thamnophilus doliatus*)	1	R
Rufous-breasted Spinetail (*Synallaxis erythrothorax*)	8	R
Rose-throated Becard (*Pachyramphus aglaiae*)	2	M
Dusky-capped Flycatcher (*Myiarchus tuberculifer*)	2	M
Unknown Flycatcher (*Empidonax* sp.)	1	R
Least Flycatcher (*E. minimus*)	11	?
Yellow-olive Flycatcher (*Tolmomyias sulphurescens*)	1	R
White-throated Spadebill (*Platyrinchus mystaceus*)	1	R
Unknown Pewee (*Contopus* sp.)	3	?
Common Tody-flycatcher (*Todirostrum cinereum*)	4	R
Mangrove Swallow (*Tachycineta albilinea*)	1	R
Barn Swallow (*Hirundo rustica*)	17	M
Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)	3	M
Rufous-naped Wren (*Campylorhynchus rufinucha*)	4	R
Swainson's Thrush (*Catharus ustulatus*)	4	M
Clay-colored Robin (*Turdus greyi*)	25	R
Bell's Vireo (*Vireo bellii*)	1	M
Tennessee Warbler (*Vermivora peregrina*)	1	M
Black-and-White Warbler (*Mniotilta varia*)	1	M
Magnolia Warbler (*Dendroica magnolia*)	2	M
Yellow Warbler (*D. petechia*)	22	M
MacGillivray's Warbler (*Oporornis tolmiei*)	2	M
Kentucky Warbler (*O. formosus*)	1	M
Hooded Warbler (*Wilsonia citrina*)	1	M
Worm-eating Warbler (*Helmithers vermivorus*)	1	M
Ovenbird (*Seiurus aurocapillus*)	3	M
Northern Waterthrush (*S. noveboracensis*)	10	M
Common Yellowthroat (*Geothlypis trichas*)	16	M
Yellow-breasted Chat (*Icteria virens*)	8	M
American Redstart (*Setuphaga ruticilla*)	1	M
Northern Oriole (*Icterus galbula*)	1	M
Blue-gray Tanager (*Thraupis episcopus*)	4	R
Painted Bunting (*Passerina ciris*)	15	M
Indigo Bunting (*P. cyanea*)	4	M
White-collared Seedeater (*Sporophila torqueola*)	28	R
Blue-black Grassquit (*Volatina jacarina*)	9	R
Grayish Saltator (*Saltator coerulescens*)	1	R

ration of the mist-net data is highly suggestive that there is indeed a greater density of birds in the riparian corridors than in the secondary forest patch.

Discussion.—Our results suggest that lands already under use for cattle ranching should not simply be written off as lost by conservation advocates; riparian vegetation corridors and other marginal habitat patches on cattle ranches can be valuable habitat refuges for a large variety of migrant and resident species. Although large-scale clearing of forest for cattle ranching is surely disastrous to many birds, as well as other animal and plant species, in an area like the Pacific lowlands of Guatemala, where virtually all of the forest has already been cleared (Universidad Rafael Landívar 1987), there may still exist valuable conservation opportunities.

In the region where we conducted our study, there exists a wide variety of land management strategies on different cattle ranches and farms; some allow relatively lush corridors of vegetation and overstory trees to grow along irrigation canals and fence lines, while others bulldoze virtually all vegetation. These differing practices surely have an enormous impact on bird communities. Even at Finca Caobanal, riparian corridors are massively cut back once or twice a year; the seasonal timing of this event may profoundly affect the suitability of the area for overwintering migrants or the nesting success of residents.

Conservation advocates in North America as well as Central America must concern themselves not only with securing the last, isolated parcels of undisturbed habitat for preservation, but just as importantly, with influencing land-management practices on lands that have already been modified by humans. Future research should provide a basis for prescribing beneficial management practices, so that the harm done in clearing forests for cattle ranching or agriculture is mitigated to the greatest extent possible.

Acknowledgments.—We thank Francois and Nini Berger and FUNDAVES for hosting us at Finca Caobanal. Ann T. Brice of the Psittacine Research Project at U.C. Davis provided financial and logistical support, and W. W. Weathers provided helpful criticism on the manuscript. This project was supported in part by U.S.A.I.D. Science and Technology Grant HRN-5600-G-00-216-00 to ATB.

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Wilson Bull., 108(1), 1996, pp. 170–175

Ungulate ectoparasite removal by Black Caracaras and Pale-winged Trumpeters in Amazonian forests.—Interspecific interactions in which an organism eats the ectoparasites of another, usually larger, organism (sometimes referred to as "cleaning symbioses"; Wittenberger 1981) comprise a relatively common form of mutualism. In terrestrial vertebrates, these associations are chiefly represented by a few bird species which routinely remove ticks and hematophagous diptera from large mammals. Such interactions, however, are by no means regularly distributed across different macrohabitats and appear to be more common in tropical savannas where recent radiations of large herbivores and their parasites are most impressive. Cleaning mutualisms are thus perhaps best illustrated by certain savanna bird species of sub-Saharan Africa such as Yellow-billed (*Buphagus africanus*) and Red-billed oxpeckers (*B. erythrorhynchus*) which are highly specialized in plucking ticks from a wide range of wild and domestic ungulate hosts for the mainstay of their diet (Attwell 1966, Bezuidenhout and Stutterheim 1980, Hart et al. 1990). In other open habitats, similar interactions also occur less frequently, for example, between Fan-tailed Ravens (*Corvus rhipi-*

durus) and camels (*Camelus dromedarius*) (Lewis 1989), Pale-winged Starlings (*Onychognathus nabouroup*) and mountain zebras (*Equus zebra*) (Penzorn and Horak 1989), Black-billed Magpies (*Pica pica*) and moose (*Alces alces*) (Samuel and Welsh 1991), and Yellow-bellied Bulbuls (*Alophoixus phaeocephalus*), and klipspringers (*Oreotragus oreotragus*) (Roberts 1993). Cattle Egrets (*Bubulcus ibis*) are perhaps the best known case of open-habitat cleaning mutualists in the New World (Burger and Gochfeld 1982), but here domestic bovid herds have largely replaced the aborigine megaherbivores with which this species was formerly associated.

In comparison, documented cases of avian species conducting similar lifestyles under close-canopy tropical forests are apparently rare. It remains to be seen, however, whether this should be attributed to the fact that (1) these habitats support far fewer species and lower densities (or smaller surface area) of large-bodied terrestrial herbivores, or (2) far less is known about the behavior and interspecific associations of forest vertebrates. Here I report two distinct cases of previously undocumented bird-ungulate mutualistic interactions observed at different Amazonian forest sites. The bird species involved in these interactions are the Black Caracara (*Daptrius ater*) and Pale-winged Trumpeter (*Psophia leucoptera*) which were observed providing "cleaning" services to Brazilian tapirs (*Tapirus terrestris*) and gray brocket deer (*Mazama gouazoubira*), respectively. Moreover, despite the disparate ecological and phylogenetic differences between these bird species, it is suggested that these interactions may be consistent throughout much of the Amazon basin.

Black Caracaras are small (330–445 g) raptors more closely related to polyborine falcons rather than to true falcons and hawks (Griffiths 1994). The Black Caracara is widely distributed throughout the Amazon basin from the eastern slopes of the Andes east to Maranhão, north to the Guianas, and south to the woodland fringes of northern Mato Grosso, Brazil. In Brazilian Amazonia, this species is more commonly found along rivers, forest edges, and associated habitats than in vast undisturbed areas of unflooded (terra firme) forest interior far removed from large rivers (Peres and Whittaker 1991, unpubl. data). Small family flocks of 3–5 individuals are often seen along rivers where they scavange primarily on small carrion, prey on arthropods and nestling birds, and occasionally feed on ripe fruit pulp (Brown and Amadon 1968, pers. obs.). *Daptrius ater,* therefore, diverges from its widely sympatric congener, the Red-throated Caracara (*D. americanus*), which is more social, far more frugivorous, but also specializes on raiding collonial wasp and bee nests (Thiollay 1991, pers. obs.).

Black Caracaras were observed cleaning a tapir on 12 September 1993 (late dry season) along a small stream draining a "cacaia" (i.e., water-logged forest patch where trees undergo a sudden die-off following a change in stream channel) on the right bank of the upper Tarauacá river, western Acre, Brazil (9°23′S, 71°54′W). A field assistant and I saw a group of eight Black Caracaras, ca 25 m from us, immediately next to an adult male tapir. An additional 10 or more caracaras were perched in the understory nearby, apparently awaiting their turn to descend upon the tapir. The tapir partly exposed its ventral parts and one of its inner hind-thighs, while lying on its side in a rather relaxed posture. The single juvenile and several adult caracaras (differentiated by the lemon-yellow and bright-orange facial skin, respectively) were actively searching for and plucking ticks attached to the large tapir which was later determined to be a bull. Four of these caracaras were searching for and grooming ticks while perched directly on top of the tapir. Another bird meticulously inspected the ventral side of the tapir between its front- and hind-quarters, whereas a third caracara partly circled around the back and dorsal flanks of the tapir, also examining its body surface. We were unable to observe whether the other caracaras were also foraging in this manner, for they were obstructed from view on the opposite side of the tapir. Upon detecting our pres-

ence 4–5 min later, all caracaras suddenly retreated to nearby perches, thus startling the tapir which immediately got up and fled from us through Maranthaceae-dominated undergrowth.

Interviews with subsistence hunters of three local communities of different parts of the Brazilian Amazon—Kaxinawá Indians of the Rio Jordão Reserve in western Acre, Kayapó Indians of A'Ukre, southeastern Pará, and caboclo (non-tribal) hunters of Vila Moura, upper Tefé river, central Amazonas—revealed that the associations between Black Caracaras and tapirs witnessed in the upper Tarauacá also occurred at these forest sites. Cleaning sessions in the upper Xingú basin (Rio Riozinho), as reported by Kayapó warriors, usually involve one adult tapir and 3–4 *D. ater,* and may last several hours while tapirs "roll over on both sides to facilitate tick removal from all body parts". Most intriguingly, experienced Kayapó hunters reported that tapirs and Black Caracaras typically are able to approach one another through a series of vocal exchanges (whistles in the case of tapirs; rasping calls in the case of *D. ater*), which apparently helps to coordinate their encounters within a closed-canopy habitat where visibility is inherently poor. Both Black Caracaras and tapirs, however, are reported to discontinue counter-calling and to remain very quiet once they eventually get to within sight of one another and during actual cleaning sessions. Indeed, hunters well aware of such rallying calls have reported cueing onto vocalizations of Black Caracaras suspected of "searching for tapirs" in order to home in on a potentially easy kill, for tapirs are the largest-bodied and often most preferred game species of native Amazonians. Should the occurrence of such mutual "approach calls" be confirmed, they would suggest that such cleaning mutualism between Black Caracaras and tapir is relatively stable and has a long history. Interestingly, both Black Caracaras and tapirs are more commonly found in river-edge, backwater palm swamps, and river- or stream-disturbed habitats, rather than in high terra firme forest on well drained soils (e.g., Bodmer 1990, Peres in press). Furthermore, Black Caracaras have not been reported to pick ticks from any other Amazonian ungulate, which perhaps suggests a high degree of specificity in these associations.

The second set of observations involves a group of trumpeters (Psophiidae), which are highly social, large-bodied (ca 1200 g), terrestrial frugivore-insectivore birds foraging almost entirely on the forest leaf-litter. The three recognized species of trumpeters White-winged Trumpeter (*P. leucoptera*), Green-winged Trumpeter (*P. viridis*), and Gray-winged Trumpeter (*P. crepitans*) are of widespread occurrence in Amazonian and the Guianan Shield forests, and comprise the only representatives of the entire family Psophiidae. Closed membership monospecific groups of 4–10 individuals maintain relatively large, stable territories which are actively defended against neighboring groups (Sherman 1991). I made these observations at a remote terra firme forest 4 km inland from the headwaters of the Urucu river, Amazonas, Brazil (4°50′S, 65°16′W). Trumpeter group size at this site averaged 6.2 individuals (N = 12). On the morning of 26 September 1988 (late dry season), as I sat under a stationary group of woolly monkeys (*Lagothrix lagotricha cana*), I observed an approaching group of seven White-winged Trumpeters walking slowly alongside an adult male Gray Brocket Deer (*Mazama gouazoubira*). Four of those trumpeters immediately next to the deer were clearly gleaning over specific parts of its pelage surface from ground level while striving to maintain fixed positions relative to the front- or hind-quarters of this cervid. Horse flies (Diptera: Tabanidae) of 15–25 mm swarming around the brocket deer were being rapidly snatched by the trumpeters through precise pecking and neck-stretching maneuvers, some of which involved a quick upward leap off the ground. I observed three tabanids beeing successfully, captured by two different trumpeters during an observation period of 45 sec. Moreover, I suspect that ticks which may have been attached to the deer (which unfortunately could not be resolved through a pair of 10 × 40 Zeiss binoculars) were also being removed and eaten: several pecks were directed at specific leg and ventral parts of the animal for no other obvious reason. Once the birds and the deer had already cleared the

nearest distance between their path and the point where I had been sitting, one of the birds sounded an alarm call, presumably directed at me. This clearly triggered the deer to sprint away in leaps and bounds, and the typical collective response of trumpeters under contexts of predation threat, which involves increased group vigilance and alarm-calling, followed by a rapid withdrawal from the source of threat once it has been identified (pers. obs.).

As suggested by several interviews, both sets of observations reported here may have a more widespread occurrence across the geographic distribution of *Daptrius ater* and *Psophia* spp. in Amazonia. Of particular interest, Sick (1984) named *Daptrius ater* as "Gavião-de-Anta" ("tapir-hawk"), but although he reports that this species "sometimes removes ticks and maggots from wild animals" (my translation), he does not specify which species of "animals" those might actually be. The larger, more terrestrial and better known relatives of forest caracaras (*Milvago*), which typically inhabit cattle-raising districts and savannas farther south, also engage in similar interactions with other species of large mammals. Yellow-headed Caracaras (*Milvago chimachima*), for instance, are well reknowed to be professional "tick-eaters", frequently picking ectoparasites off livestock and capybaras (*Hydrochaeris hydrochaeris*) in the Brazilian pantanal and cerrado (Sick 1984, F. Olmos, pers. comm.). *M. chimachima* and a number of other avian species which remove ectoparasites from large mammals (e.g., magpies: Goodwin 1986) can, however, take advantage of these associations to nibble at flesh and, therefore, maintain or enlarge branding wounds on their mammalian hosts (Brown and Amadon 1968). Although this clearly brings nutritional advantages to these birds, it remains to be determined whether or not *Daptrius ater* and *Psophia leucoptera* "cheat" in these otherwise mutualistic interactions by also eating live tissue from open sores.

At oxbow lake- and river-edge habitats along white-water rivers of western Amazonia, Giant Cowbirds (*Scaphidura oryzivora*) are commonly observed catching tabanid flies, and perhaps ticks, parasitizing capybaras (J. Terborgh, pers. comm.), and Robinson (1988) once observed a Giant Cowbird foraging on the back of a tapir. One of the few other cases of ectoparasite removal from *Tapirus* was reported for white-nosed coatis (*Nasua narica*) grooming a few individuals of Baird's tapirs (*T. bairdii*) near the Barro Colorado Island Field Station in Panamá (McClean 1992). This interaction, however, was apparently learned locally and represented a human artefact in that both species had been routinely fed in the laboratory clearing, and thus spent a disproportionately large amount of time together.

The three-way interactions reported here, although easily overlooked in forest habitats, may be of great importance to hematophagus arthropods, large mammalian hosts, and bird species, such as caracaras and trumpeters, which successfully take advantage of such foraging opportunities. Ticks and tabanid flies, particularly if engorged with a full bloodmeal, may represent a key nutritional supplement to the birds. For the ungulate hosts, too, this may represent the most efficient way of eliminating unwelcome ectoparasites, which could serve as vectors of major debilitating diseases. Of special interest, Amazonian forest ungulates, such as tapirs, both brocket deer species (*Mazama americana* and *M. gouazoubira*) and peccaries (*Tayassu tajacu* and *T. pecari*) appear to be particularly susceptible to infestations of large ticks. Hunters throughout the region often report examining carcasses of these species with conspicuous ectoparasite loads, suggesting that infestation rates may be faster than removal rates by mutualists or spontaneous withdrawal of the ectoparasite. In the case of tapirs, kills are reported either to be heavily infested with ticks or conspicuously "clean" (carrying no ticks), which suggest that tick-removal bouts by avian mutualists may be relatively sporadic. Indeed, several species of ungulate may lose physical condition if subject to chronic ectoparasite infestations, but whether or not such associations depress ectoparasite populations to any significant extent is yet to be determined (but see Samuel and Welsch 1991). Indeed, greater population densities of open-habitat mutualists (such as

that of Yellow-headed Caracaras in central Brazil) appear to be available to provide ectoparasite removal services to savanna and forest-edge grazers than are their equivalent forest species to browser-frugivore ungulates. Perhaps the evolutionary opportunity presented by the inherently low densities (and smaller body surface area) of forest megaherbivores—which could otherwise subsidize larger populations of large-bodied hematophagous arthropods—was never significant enough to be claimed by cleaning mutualists more specialized than caracaras and trumpeters.

Acknowledgments.—The faunal inventories which made these observations possible were funded by the Wildlife Conservation Society and the Brazilian Science Council (CNPq). I thank Josimar Pinheiro (Kaxinawá), Karuro and Batión (Kayapó), and Edvar Dias for their valuable assistance during fieldwork at sites surveyed in the upper Tarauacá, upper Xingú, and upper Tefé rivers, respectively.

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Wilson Bull., 108(1), 1996, pp. 175–178

Notes on the status and behavior of the Swainson's Warbler in Cuba.—The Swainson's Warbler (*Limnothlypis swainsonii*) is one of the less common North American warblers (Morse 1989). Although data from the Breeding Bird Survey suggest that the species has undergone a significant range-wide population increase during the period 1966–1988 (Sauer and Droege 1992), regional Neotropical migrant prioritization schemes for the midwestern (Thompson et al. 1993) and southeastern (Hunter et al. 1993) United States consider the Swainson's Warbler among the more vulnerable Neotropical migrants based on its low population, threats on the breeding and wintering grounds, and its restricted range. Considering its vulnerability, the status of the Swainson's Warbler is poorly known in its breeding range (Hunter et al. 1993), and even more so in winter. Here, we summarize recent and historical records for the Swainson's Warbler in Cuba, re-assess its status there, and describe aspects of its foraging and flocking behavior based on casual observations, previously published information, and anecdotal reports.

The Swainson's Warbler winters in the northern Bahama Islands, Cuba, the Cayman Islands, Jamaica, the Yucatán Peninsula, and Belize (AOU 1983). There are also sight and banding records from Puerto Rico (AOU 1983; J. Faaborg, pers. comm.) and sight records from St. John (Raffaele 1989). It is reported as casual on the Swan Islands (AOU 1957). In Cuba, the Swainson's Warbler has been considered a rare winter resident (Garrido and García Montaña 1975). The first report for Cuba was provided by Gundlach (1876) who knew of a single sight record from La Habana (Fig. 1). In the 150 years prior to 1991, it is unknown exactly how many Swainson's records exist for Cuba, but we are aware of only 21 (Fig. 1).

Banding activities carried out during the winters of 1991–1994 by Cuban researchers of the Institute of Ecology and Systematics (IES) of the Ministry of Science, Technology, and Environment, the Cuban National Museum of Natural History; and by a cooperative forest bird survey project of the IES, the Canadian Wildlife Service (CWS), and the Long Point Bird Observatory (LPBO) have provided many new records of Swainson's Warbler. Recent bird-watching tours have contributed additional sight records of the species. In total, 58 individuals were observed, netted, or collected at 17 sites during the winters of 1991–1994 (Fig 1). Highest numbers were at El Cenote, Ciénaga de Zapata, Matanzas Province, where 13 (1.80/100 net-h) were captured 11–14 February 1991, and at Camino al Sitio Viejo, Cayo Coco, Ciego de Avila Province, where 12 (1.67/100 net-h) were captured 27–30 January 1994. Seasonally, Swainson's Warblers have been observed in Cuba from 15 September to 14 April (Garrido and García Montaña 1975; Garrido and Kirkconnell, unpubl. data).

Historical and recent Cuban records indicate that Swainson's Warblers occur in the lowlands, montane regions, and in swampy areas. They apparently prefer semideciduous forest with high shrub and tree stem density, complete, or nearly complete, canopy cover, abundant

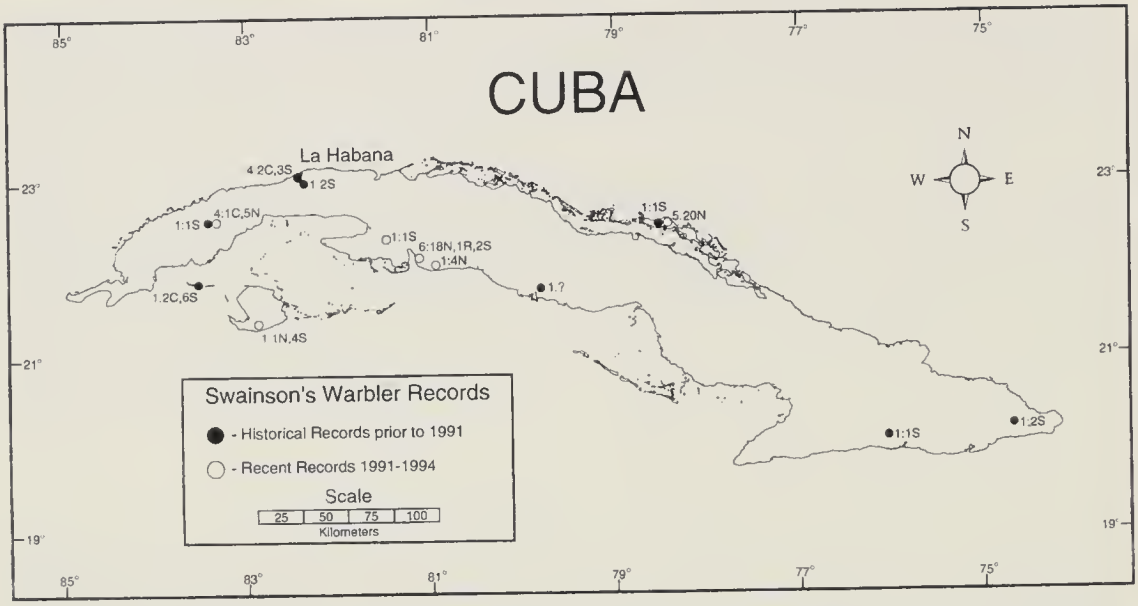

FIG. 1. Distribution of historical and recent records of the Swainson's Warbler in Cuba. The first numeral, followed by a colon, indicates number of sites at that location from which records are derived and is followed by the number of individuals in each of the following categories: C = Collected, N = Netted and usually banded, R = Recapture of bird banded previous year, S = Sight record, ? = exact number of individuals unknown.

dry leaf litter, and humid, shady areas, sometimes near streams, or near waterholes in limestone bedrock near the coast. While they seem to inhabit mostly larger forest tracts, they also occasionally reside in smaller forest fragments in the vicinity of larger forests, or, in the keys, in patches of low coastal scrub.

Inter-winter site fidelity has been documented for the Swainson's Warbler in Jamaica (Diamond and Smith 1973). In the recent Cuban banding surveys, a Swainson's Warbler was recaptured one year after banding and 120 m from the original capture site (McNicholl 1992).

Swainson's Warblers spend most of their time on the ground or less than 1-2 m above it. Lack and Lack (1972) reported that Swainson's Warblers in Jamaica always feed on the forest floor where they rummage and probe in leaf litter, sometimes tossing leaves aside. Our observations in Cuba support this, but include sightings of the species insect gleaning from surfaces of leaf litter or bare ground, and gleaning prey in slow moving water. Whereas insects seem to be the principal food items, Eaton (1953) discovered the bones of small lizards, perhaps anoles (*Anolis* sp.) or geckos (*Sphaerodactylus* sp.), in stomach samples of Swainson's Warblers wintering in Cuba.

Although Eaton (1953) classified Swainson's Warblers as solitary foragers, we frequently observed them foraging in close association with other warblers, particularly Ovenbirds (*Seiurus aurocapillus*) and Worm-eating Warblers (*Helmitheros vermivorus*). When the three species were together, Swainson's Warblers foraged in the wettest areas with Worm-eating Warblers, while Ovenbirds foraged in drier areas. At La Güira, Pinar del Río Province in Feb-Mar 1986, Garrido twice observed Kentucky Warblers (*Oporornis formosus*) and Hooded Warblers (*Wilsonia citrina*), joining such mixed-species flocks, typically feeding within a few inches of the ground, and sallying or hovering in a manner similar to the American Redstart (*Setophaga ruticilla*) (Bennett 1980).

In many of our sightings, we observed an apparent association between Swainson's Warblers and Ovenbirds. Like Swainson's Warblers, Ovenbirds pick insects off leaf litter or the

ground, but, in general, they use their bills to rummage in dry leaves more frequently than Swainson's Warblers. During four of our sightings, we observed a Swainson's Warbler feeding in the "wake" of an Ovenbird, sometimes following the Ovenbird within a few centimeters. During many other observations Ovenbirds and Swainson's Warblers foraged in close proximity without any apparent aggression. Ovenbirds and Swainson's Warblers were frequently captured side-by-side in mist nets suggesting that they were moving together through the forest. We suggest that the body movements of walking Ovenbirds, which often include repeated cocking of the tail, and the disruption of the leaf litter with the bill and feet, make otherwise cryptic insects move or fly, facilitating their capture by Swainson's Warblers (the "beater effect" of Powell 1985). Other potential explanations of this trailing behavior include the possibility that active foraging by Ovenbirds signals the presence of food resources to Swainson's Warblers, as proposed for a variety of mixed-species assemblages (e.g., Gannon 1934, Rand 1954, Sealy 1973, Turner 1965); or that the association provides enhanced predator detection for both species, as proposed for other mixed-species flocks (e.g., Cody 1971).

In summary, the recent evidence provided by bird banding and regular, intensive searching during bird-watching tours suggests that the Swainson's Warbler is a more common winter resident in Cuba than previously believed. The total of 58 individuals recorded during the winters of 1991–1994 is nearly three times the total recorded in the previous 150 years. We believe that the paucity of early records is attributable to the cryptic plumage of the species, its elusive behavior in dense vegetation, and, particularly, the lack of intensive surveys utilizing mist nets.

Acknowledgments.—We thank the Cuban Ministry of Science, Technology, and Environment, the Canadian Wildlife Service, Great Auk Nature Tours, Long Point Bird Observatory, and the Canadian Nature Federation for financial and logistical support. Graeme Gibson of Great Auk Nature Tours and CubaTour made the bird-watching trips to Zapata and La Güira possible. The following people assisted in the field: Martín Acosta, Vincente Berovides, Pedro Blanco, Jane Bowles, Beverly Collier, Ronel Concepción, Donald Fillman, Esteban Godinez, Raúl Gómez, Hiram González, Colleen Hyslop, Judith Kennedy, Alejandro Llanes, Frank Loyola, Miriam Martinez, Jonathan McCracken, Martin McNicholl, Lourdes Mugica, Ramona Oviedo, Alina Pérez, Ronald Ridout, Daysi Rodríguez, Bárbara Sánchez, Eliser Socarrás, Steven Wendt, and Daily Zuñiga. Joseph Walter of the Geographic Resource Center, Univ. of Missouri produced the map. Michael Baltz, John Faaborg, Herbert Raffaele, Elizabeth Wallace, and an anonymous reviewer contributed valuable comments on the manuscript.

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Wilson Bull., 108(1), 1996, pp. 178–180

Comments on a probable gynandromorphic Black-throated Blue Warbler.—Sexual plumage differences in passerine birds are believed to be controlled genetically and only minimally influenced by hormones (Murton and Westwood 1977). Bilateral gynandromorphs are among the most striking manifestations of chromosomal regulation of plumage (Crew and Munro 1938, Cock 1960, Witschi 1961). In these rare individuals, plumages of the left and right sides of the body are demarcated along the midline and presumably reflect gonadal placement. In most cases, an ovary and female plumage are found on the left side, a testis and male plumage on the right. Several hypotheses have been advanced to explain the

genesis of gynandromorphs and mosaics, but it is possible that several genetic mechanisms or ontogenetic tracks may produce a variety of phenotypic outcomes collectively lumped as bilateral gynandromorphs. This idea is suggested by variation in the degree of plumage asymmetry in gynandromorphs. For example, traces of definitive male plumage may appear on the "female" side and vice versa (e.g., Laybourne 1967). One problem with categorizing gynandromorphic birds, is that there are no standard conventions of analysis, such as those developed for diagnosing hybrids (Graves 1990). The following example illustrates some of the difficulties.

Patten (1993) reported an unusually plumaged Black-throated Blue Warbler (*Dendroica caerulescens*) that was photographed but could not be collected at Stovepipe Wells, Death Valley National Monument, Inyo County, California, in October 1987. Patten described (p. 696) this individual as "sexually dimorphic with respect to each lateral half of the bird, with the left side appearing to be male and the right looking like a female." While we believe the bird was correctly identified as a bilateral gynandromorph, the first such record for the subfamily Parulinae, a reappraisal of photographs suggests that its phenotype was qualitatively different from bilateral gynandromorphs previously reported among passerines (Crew and Munro 1938, Kumerloeve 1987).

We examined two color transparencies taken by Dunn (Visual Resources for Ornithology [VIREO] archives catalog numbers v06/23/001–v06/23/002) as well as those examined by Patten (taken by Paul E. Lehman, VIREO v06/12/001–v06/12/004). The left side of the bird appears to be in male first-basic plumage (hatching year), as indicated by brownish secondaries and primaries and an unusual white spot on the lower eyelid. The left side is clearly demarcated from the right side along the midline of the mantle. The right side has an enigmatic appearance not matched by any of the 1370+ study specimens of Black-throated Blue Warbler in the National Museum of Natural History (USNM), Smithsonian Institution. The principal characters of the right side include (1) pale supercilium that extends from the base of the bill posteriorly to the rear of the auriculars where it becomes broader, (2) extensively white lower eyelid, (3) grizzled black and white throat, whiter at the center, (4) pale malar mark, (5) yellowish wash on the belly and lower sides, (6) a relatively wide black stripe on the side that extends from the lower edge of the throat posteriorly past the bend of the wing to the base of the primary coverts, (7) large white triangle at the base of the primaries, and (8) mantle and crown, olive-gray, distinctly less "blue" than the left side.

A comparative description of the right side of this gynandromorph and basic plumages of male and female Black-throated Blue Warblers follows. White superciliary and lower eyelid markings occur rarely in fall male Black-throated Blue Warblers in first basic plumage but are unknown in males in definitive basic plumage. In contrast, nearly all females have pale superciliaries and lower eyelid spots (see Parkes 1979). The face pattern of Patten's bird was more strongly pronounced than that of any male or female we have examined.

Throat feathers of males in first basic plumage are often tipped with white, imparting a grizzled appearance. With very rare exceptions, females have unmarked throats. Patten's bird had a grizzled throat, whiter near the center, and a pale malar mark, thus appearing more male-like than female in this character.

A black stripe extends from the side of the throat posteriorly along the sides to the lower flanks in basic-plumaged males, whereas females in all plumages have unmarked sides. Patten's bird exhibited a distinctive black stripe that began at the right side of the throat and continued to the upper flanks, becoming more diffuse posteriorly. The extent of the black stripe was well within the range exhibited by males in first basic plumage. The remainder of the underparts of Patten's bird more closely resembled those of females in basic plumage.

In sum, the right side of Patten's bird appeared to be a mosaic of distinctive elements from both male and female plumages, but weighed more heavily toward male characters,

while the left side was typically male. However, the true nature and cause of this plumage asymmetry will never be known without a specimen.

Crew and Munro (1938) concluded that bilateral gynandromorphism in birds is of three types: (1) the finch or sparrow type where plumage is genetically determined and reflective of lateral chromosome distribution; (2) the chicken or fowl type in which sexual differences in plumage are subject to hormonal regulation so that perfect bilaterality of plumage is impossible; and (3) the pheasant type where plumage on one half of the bird is normal and the other half is an intersexual mosaic (Danforth 1937a,b). Nearly forty years later, Hollander's (1975) review of sectorial mosaics in pigeons suggested that mosaics of sex-linked plumage may be caused by bipaternity and the subsequent incorporation of tissue derived from supernumerary sperm into an embryo. This process may result in an asymmetrical patchwork of male and female plumage such that one side appears to be normal and the other side an intersexual mosaic. In any case, little has been learned about gynandromorphism in passerines other than the fact that departure from bilateral asymmetry is variable (see Laybourne 1967, Kumerloeve 1987). The appearance of Patten's bird, normal male on the left side and intersexual mosaic on the right, marks an observed extreme within the order Passeriformes.

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Wilson Bull., 108(1), 1996, pp. 181–182

Rufous crown feathers on adult male Tennessee Warblers.—The presence of rufous crown feathers in Tennessee Warblers (*Vermivora peregrina*) is an undescribed feature that supports taxonomic affinities with other *Vermivora* warblers, although the possibility of hybrid origins exists. In 1980, among Tennessee Warblers collected from Aquatuk Lake in northeastern Ontario, J. A. Dick noted two adult males with crown feathers with some rufous coloration among the normally grayish crown feathers. This phenomenon seems to have been overlooked in descriptions of this species, except for a very brief passing comment by Chapman (1917). S. V. Nash and R. D. James located another example in northeastern Ontario in 1982. The Royal Ontario Museum has six additional birds displaying some rufous in the crown. This note describes in greater detail the extent of rufous crown feathers in Tennessee Warblers.

J. A. D. asked curators of several other North American museums, if they had Tennessee Warblers with rufous crown feathers. Nine of 850 (about 1%) were reported to have them. The proportion may be higher, as the coloration can be overlooked easily (see below) and in Royal Ontario Museum collections eight examples among 136 specimens (nearly 6%) show some rufous on crown feathers.

The rufous feathers, as is typical of other *Vermivora,* are found on adult males that normally have completely gray crowns. On any individual feather, the rufous is in the center of the feather, including the rachis, although one vane may be more highly colored. It may be fairly distinct and roughly tear-drop shaped, and the gray distal border of the feather is as wide as the rufous drop. Thus, the rufous might be scarcely, if at all, visible when the feathers are in place, as only the gray terminal edges of the feathers would show. On some other birds, the rufous is much less distinct, being a very light suffusion among the gray, and extends closer to the distal ends of the crown feathers. This type is usually visible with the feathers in place but can be so pale as to be scarcely noticeable.

The rufous color is not as orange as on an Orange-crowned Warbler (*V. celata*), nor as chestnut as on a Nashville Warbler (*V. ruficapilla*). It is somewhat intermediate, but more orange than chestnut. It approximates the orange-rufous of Smithe (1975), color 132C, but is very much paler than that illustrated, making it easy to overlook. The number of colored feathers also varies considerably from bird to bird. Some have only one or a very few, usually close to the front center of the crown and usually, but not always, the more strongly colored; one bird had only a single very pale colored feather. The paleness and the small numbers and size of the feathers makes them difficult to detect. On several others there were numerous colored feathers, usually less intensely colored and lying in a "patch" across the center to hind crown. The rufous coloration becomes more obvious if the feathers are ruffled to show the length of individual feathers. But it is also possible that the rufous color has faded on the older specimens, making them even more difficult to detect. One bird showed some stronger coloring toward the front center as well as more lightly colored feathers toward the back of the crown. Another showed a suffusion of color across only the fore crown, strongest toward the front center.

There is only one known hybrid specimen involving the Tennessee Warbler, Carnegie Museum of Natural History 152341, collected at the museum's Powdermill Nature Reserve, Rector, Pennsylvania, on 26 August 1979. The other putative parent species was identified by K. C. Parkes and R. C. Leberman as the Nashville Warbler, a species in which adult males have an obvious rufous crown patch. The hybrid specimen, however, is a male in first basic plumage. Although 70% of males of *V. r. ruficapilla* of this plumage stage in the Carnegie collection have crown patches, the patches are unknown in young Tennessee Warblers, and there is no sign of one in the hybrid (K. C. Parkes, in litt.). Intrageneric hybrids

are rare in the Parulinae (Parkes 1978; Bledsoe, 1988), and it would seem unlikely that the crown patch in Tennessee Warblers is a consequence of hybridization. None of those we have examined with rufous crown feathers would appear to be anything but typical Tennessee Warblers in other respects. With more than one percent of the population exhibiting rufous crown feathers, it seems much more likely that the rufous is a vestigial plumage pattern of the type typically found in most other members of the genus *Vermivora.*

Among other *Vermivora* warblers in which the males exhibit obvious rufous crown patches, it might be presumed that these patches serve a display function. It seems very unlikely, however, that the coloration now serves any display function in Tennessee Warblers, since it is either very restricted or very pale.

Acknowledgments—We thank S. V. Nash for assistance in the field. S. F. Bailey, Univ. of California, Berkeley, J. W. Fitzpatrick, Field Museum of Natural History, J. Hinshaw, Univ. of Michigan, Ann Arbor, H. Ouellet, Canadian Museum of Nature, K. C. Parkes, Carnegie Museum of Natural History, and T. Webber, Florida State Museum kindly examined specimens in their respective institutions for us. We would also like to thank K. C. Parkes and J. D. Rising for comments on an earlier draft of this paper.

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Wilson Bull., 108(1), 1996, pp. 182–186

American Goldfinch nests in purple loosestrife.—Bird foraging, nesting, and other activities are often closely related to vegetation characteristics. Introduced plants may alter the architecture and chemistry of the plant community, potentially affecting the food base and nest substrate available to birds. One non-indigenous plant, purple loosestrife (*Lythrum salicaria*), is said to have little value to North American wildlife, and a biological control program is predicted to dramatically reduce American populations of loosestrife (Malecki et al. 1993). Here I report American Goldfinch (*Carduelis tristis*) use of loosestrife as nest substrate.

The American Goldfinch is a widespread breeding bird in North America and nests in a variety of habitats that include parks and yards with ornamental vegetation, weedy waste grounds, forest edges, fence rows, old fields, abandoned orchards, shrub swamps, and marshes. Nickell (1951) and Smith (1988) suggested that pre-Columbian habitats were beaver

TABLE 1
AMERICAN GOLDFINCH NESTS IN PURPLE LOOSESTRIFE, SOUTHEASTERN NEW YORK

Dimension	Mean	Median	IQR[b]	Range	N
Nest rim to soil (cm)	140.3	134	121–182	90–190	7
Plant height from soil (cm)	229.7	224	200–246	192–315	7
Nest height fraction of plant height (%)	60.9	60.3	54–66.7	45–74	7
Maximum plant diameter at level of nest (cm)	94.2	94	67–114	58–152	12
Nearest woody plant >1 m tall (m)[a]	14.6	11.5	6.5–21	2–34	12
Nearest open water >1 m wide (m)[a]	9.2	4	1–16	1–37	11
Nearest shore (upland) (m)[a]	19.4	17	0–29	0–71	11

[a] Paced or estimated from maps.
[b] Interquartile range.

meadows, wetlands, lake and river banks, and burn areas. Purple loosestrife, a robust, shrub-like forb introduced to North America ca 1800 (Thompson et al. 1987), is common in the moister types of habitats used by nesting goldfinches in New York.

From 1971 to 1994, in the course of other field work, I found 15 American Goldfinch nests in purple loosestrife in Dutchess and Ulster counties in the Hudson Valley (Table 1). I have deposited voucher photographs at Visual Resources for Ornithology (VIREO catalog numbers v06/22/001 through v06/22/004; Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania). Three nests were active and 12 abandoned, the abandoned nests identified by a persistent accumulation of nestling feces on the nest rim (Walkinshaw 1939, Berger 1971:258).

The goldfinch nests were above water or intermittently saturated soil as follows: five in flooded nontidal marshes, two in the upper intertidal zone of a freshwater-tidal marsh, two at pond margins, two in patches of unmowed wet meadow within mowed fields, one in a patch of wet meadow in a dry old field, two in extensive wet old fields, and one in a small roadside wetland. The nests were attached-statant and resembled types 1, 2, and 6 illustrated by Nickell (1958) for the goldfinch. The nests were typically woven around several primary vertical stems of loosestrife and their ascending secondary branches, with the branches preventing the nests from sliding down the primary stems. Nests were attached to stalks of the current year (8), previous year (1), or both years (2), and remained identifiable through one or even two winters (Smith 1988). The nests were in tall, wide, many-stemmed loosestrife clumps near or touching other robust loosestrife (Table 1). The nests were not wider than high (contra Allen 1934), probably the result of attachment to the vertical stalks of loosestrife rather than being saddled on horizontal branches of woody plants.

Goldfinch nesting habitat, nest sites (plant species), and nest height vary greatly (Berger 1971), but nests are not placed on wholly artificial substrates or on the ground (Nickell 1951). I compiled literature reports of 5991 nest substrate records, predominantly (94%) from the Great Lakes region, representing 87 plant species or genera. Of these records, 87.5% are in broad-leaved trees or shrubs and only 11.6% in herbs (almost all thistles [*Cirsium*]). The same records comprise 55% nests in plant taxa native (Gleason and Cronquist 1991, Peattie 1991) to the American Goldfinch breeding range, 1% in introduced taxa, and 44% not determinable as native or introduced (mostly hawthorns [*Crataegus*] and willows [*Salix*]). The records are 32% wetland plant taxa following the classification of Reed (1988), 22% upland taxa, and 46% ambiguous (mostly hawthorns, elms [*Ulmus*], and maples [*Acer*]). The data compilation and a list of sources have been deposited at the National

Technical Information Service (NTIS Accession Number PB95-226965; 5285 Port Royal Road, Springfield, Virginia 22161).

Nickell (1958) remarked that American Goldfinch and Red-winged Blackbird (*Agelaius phoeniceus*) are exceptions to the rule that bird species nesting above the ground do not attach nests to herbs because they are weak, insufficiently branched, and not fully grown at the peak of the nesting season. Goldfinch nests with shorter distances from woody plants (Table 1) suggest loosestrife was occasionally selected in preference to apparently suitable woody species close by, and nests with longer distances indicate loosestrife allowed goldfinches to nest in the interiors of herbaceous wetlands not otherwise usable. Purple loosestrife is intermediate in growth form between the shrubs and the thistles used by nesting goldfinches. Like the thistles, loosestrife shoots develop late; they do not reach full height until August (Rawinski 1982:27). Most goldfinches begin nest construction mid-June to mid-August. The late development of loosestrife may make it unsuitable for some marsh birds that build elevated nests in May and June.

McCabe (1991:50, 55) believed concealment from predators, weather, sunlight, and conspecifics the key factor governing taxonomic choice of nest site in the Willow Flycatcher *Empidonax traillii* Goldfinch eggs, nestlings, and sitting females are vulnerable to overheating in the sun and to chilling in rain and wind (Mayer 1981, Kleinhenz 1984). Eggs and nestlings can also drown when tightly constructed nests fill with rain (Allen 1934). Kleinhenz (1984) found that successful nests had more overhead vegetation cover, and that goldfinches selected broad-leaved rather than narrow-leaved hawthorns. Mature loosestrife has a dense leafy crown that presumably shelters goldfinch nests from sun, wind, and rain; tall, dense loosestrife growth probably also conceals nests from predators and the Brown-headed Cowbird (*Molothrus ater*).

Wetlands can be refuges from predation and brood parasitism (Kiviat 1989). Expanses of soft wet soil, stream channels, or frequent flooding may deter some mammals and snakes from reaching nests. Many potential avian predators and the Brown-headed Cowbird do not venture far into marshes that lack tall shrubs or trees. Low rates of nest predation and brood parasitism of blackbirds, Swamp Sparrow (*Melospiza georgiana*), and Song Sparrow (*M. melodia*) have been recorded in extensive marshes (Johnston 1956, Friedmann 1963, Meanley and Webb 1963, Ortega and Cruz 1991).

Native birds commonly nest in certain introduced plants, e.g., shrubby honeysuckles (*Lonicera* spp.), common buckthorn (*Rhamnus cathartica*), and multiflora rose (*Rosa multiflora*) DeGraaf et al. 1975, Whelan and Dilger 1992), whereas other aliens such as tamarisk (*Tamarix* spp.) (Brush 1983, Ohmart et al. 1988:156–157) are rarely used, and not all native species are used equally (Berger 1971:217). Although the American Goldfinch more often nests in native than introduced plants, a few abundant alien taxa are used. The breeding range of the American Goldfinch (AOU 1983) and the American range of purple loosestrife (Thompson et al. 1987:19) are nearly conterminous, making loosestrife a potential nest substrate for the goldfinch over much of its range. In extensive marshes lacking woody vegetation, loosestrife could have facilitated an ecological extension of goldfinch nesting habitat. Native forbs that form tall clumps and dense patches in marshes and wet meadows rarely provide a structure as dense, leafy, and sturdy as that of mature clumps of purple loosestrife.

Acknowledgments.—Charles Leck, Brooke Meanley, Thomas J. Rawinski, Gretchen Stevens, Bryan L. Swift, and Julie Zickefoose reviewed a draft, and I am also grateful to referees Alex L. A. Middleton, Charles R. Smith, and Doris Watt. This is Bard College Field Station - Hudsonia Contribution 31.

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Wilson Bull., 108(1), 1996, pp. 186–187

Opportunistic winter water acquisition by Pine Grosbeaks.—The sparse documentation of water acquisition by birds in cold regions is limited primarily to observations of consumption of water in a frozen form. Methods reported include Pine Siskins (*Carduelis pinus*) eating snow, Cedar Waxwings (*Bombcilla cedrorum*) catching snowflakes during a storm (both by Dr. Glover Allen as cited in Gordon (1934) and in Allard (1934)), and "Song Thrush" chipping ice (Harding 1986). Allard (1934) also reported "starlings" eating snow and catching snowflakes. Other species observed eating snow include the "Redwing (*T. iliacus*) and Blackbird (*T. merula*)" (editors note following Harding [1986]), and Bohemian Waxwing (*B. garrulus*) (pers. obs.).

This note documents the opportunistic exploitation of free water droplets in a cold region in winter by Pine Grosbeaks (*Pinicola enucleator*). It also notes that this species has the ability to hover, somewhat like a hummingbird, for short periods.

Lone Pine Grosbeaks were observed on 7 November 1992 and again 20 December 1994 at a site about 24 km northeast of Anchorage, Alaska, in Eagle River Valley (61°19′N/149°28′W), flying from a cottonwood tree (*Populus* sp.) perch to hover briefly below an icicle as a droplet of water formed. The droplet was sipped off the end of the icicle and then the bird returned to its perch in the tree about 1.5 m away. This process was repeated 5–10 times over a 5-min period. The icicles were forming off the roof of a cabin located on a south-facing 27° slope. The area is under what Viereck et al. (1992) classifies as an "open poplar" (I.B.2.c) or "open spruce-poplar" (I.C.2.d) forest and receives its first measurable snowfall in September and is snowfree by mid April (pers. obs). The area is visited intermittently throughout the winter months by Pine Grosbeaks. Temperatures prior to both observations varied somewhat (±3°C) but were consistently subfreezing ($\bar{x} = -10$°C) at night (National Weather Service, pers. comm.; NOAA 1992) and at or above freezing (0–5°C range) during the day at the 610 m elevation observation site. Both observations were preceded by snowfall of 25 cm (6–7 November 1992) (NOAA 1992) to 46 cm (15–18 December 1994) (pers. obs.). These conditions led to droplet-producing icicles along the south-facing roof pitch.

Acknowledgments.—I thank A. Carter, Alaska Bird TLC; D. Irons, USFWS; and anonymous reviewers for their helpful suggestions on the manuscript. I also appreciate the research assistance received from University of Alaska–Fairbanks and USFWS library staffs.

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Received 16 May 1995, accepted 30 Sept. 1995.

Wilson Bull., 108(1), 1996, pp. 187–189

Evidence of nest parasitism in Mottled Ducks.—Intraspecific nest parasitism, which is the fostering of one or more eggs into the nest of a conspecific, is widespread in waterfowl (Yom-Tov 1980, Eadie 1991). Intraspecific nest parasitism is most common among cavity nesting waterfowl and waterfowl that nest in colonies (Rohwer and Freeman 1989). In contrast, it is rare in solitary, upland-nesting waterfowl, including most Anatini (Eadie et al. 1988, Rohwer and Freeman 1989), except when they nest in high densities (e.g., Drewien and Fredrickson 1970, Titman and Lowther 1975, Hines and Mitchell 1984). Dense-nesting situations may facilitate parasitism by reducing the time, energy, and risk associated with finding host nests (Rohwer and Freeman 1989). Some authors (e.g., Jones and Leopold 1967, Erskine 1990) have suggested nest parasitism may also occur as a consequence of nest site competition when waterfowl nest in high densities. However, parasitism persists in cavity nesting ducks when nest sites are abundant (Semel and Sherman 1986) and evidence for nest site competition in non-cavity nesting waterfowl is equivocal (Rohwer and Freeman 1989). Intraspecific nest parasitism has been documented for only six species of Anatini from North America: Northern Shoveler (*Anas clypeata*), Green-winged Teal (*A. crecca*), Cinnamon Teal (*A. cyanoptera*), Mallard (*A. platyrhynchos*), American Black Duck (*A. rubripes*), and Gadwall (*A. strepera*) (reviewed in: Eadie et al. 1988, Rohwer and Freeman 1989, Sayler 1992). Here we report the first evidence of intraspecific nest parasitism in the Mottled Duck (*A. fulvigula*).

We found 132 Mottled Duck nests during searches of six islands in the Atchafalaya Delta Wildlife Management Area (29°26′N, 91°20′W), Saint Mary Parish, Louisiana, during March through August 1994. When we found a nest, we estimated incubation stage (Weller 1956) and individually marked all eggs. Newly laid eggs were marked on subsequent nest checks and incubation stage was estimated again. Incubation period for Mottled Ducks was assumed to be 26 days (Stutzenbaker 1988).

We found four cases of apparent nest parasitism. (1) On 8 April, we found a nest containing 12 eggs, which we estimated at 19 days incubation. On 16 April, the nest contained several recently hatched eggs and one unhatched egg. We opened the unhatched egg, which contained a 15 day-old embryo (Caldwell and Snart 1974). We believe that this was a nonterm egg (an egg laid after the onset of incubation, Morse and Wight 1969) and not an

embryo that died during development, because it had not deteriorated. (2) On 16 April, we found a laying stage nest containing 10 eggs. The nest contained 15 eggs on 29 April. Four of these eggs clearly differed in color from the rest of the clutch and were estimated to have been incubated ≤four days. Egg color difference can accurately distinguish parasitic eggs in some birds (Lyon 1993) and has been used to identify parasitic eggs in waterfowl (Jones and Leopold 1967). Egg color difference, together with an approximate eight day difference in incubation stage, suggests that the four eggs were laid by a hen other than the host. On 12 May, the nest contained 10 ducklings and eight unpipped eggs. Seven of the unhatched eggs differed in color from shells of the hatched eggs. The large clutch size (18 vs typical range of 8–13 eggs, Stutzenbaker 1988) was further evidence of nest parasitism. (3) On 7 May, we found a nest containing 12 eggs, most of which had 12-day-old embryos. Three eggs, however, differed in color from the others and were 5–10 days less developed. On 18 May, there were hatching movements (≥23 days of incubation) in all eggs except the three differently colored eggs. On 25 May, there was evidence of hatched eggs, but no intact eggs remained in the nest. (4) On 6 July, we found a laying stage nest containing six eggs. It contained nine eggs on 20 July, one of which was a different color and was unincubated (≤3 days, Weller 1956). On 30 July, the nest still contained nine eggs, several of which had hatching movements, but the off-color egg's incubation stage was 11 days. An 8 August nest check revealed evidence of hatched eggs, but two unhatched eggs remained, one of which was the egg of different color.

All four cases of suspected parasitism occurred on one 22-ha island, where most (N = 82) nests were found. The estimated parasitism rate (minimally 5%) on this island was similar to other studies of island nesting Anatini (Rohwer and Freeman 1989). We were unable to estimate nest densities because we did not systematically search islands. However, during March and April, areas searched on islands were approximately equal and twice as many nests were found on the 22-ha island as on all other islands combined. Three of the other islands were >40 ha. The other two were <20 ha and were often flooded. Failure to detect parasitism on other islands may reflect smaller samples of nests or lower nest densities.

Acknowledgments.—Financial support was provided by the Fur and Refuge Division, Louisiana Dept. of Wildlife and Fisheries. We are grateful to the Atchafalaya Delta Wildlife Management Area staff for logistical support provided during field work. P. R. Garrettson and W. L. Hohman provided helpful comments on the manuscript.

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Wilson Bull., 108(1), 1996, pp. 189–190

Eight new host species for the parasitic blow fly genus *Protocalliphora* (Diptera: Calliphoridae).—Larvae of *Protocalliphora* blow flies (Diptera: Calliphoridae) are obligate hematophagous parasites that reside in nests of birds with nidicolous young where they intermittently attach to the nestlings to feed. Only one species of *Protocalliphora, P. braueri,* is known to be an obligate subcutaneous parasite (Sabrosky et al. 1989). *Protocalliphora* blow flies appear to have little host specificity (Bennett and Whitworth 1992), and, with the exception of birds whose nest structure is not conducive to blowfly retention and development (e.g., loosely arranged stick nests, very wet nests), eventually all nidicolous bird species within the range of these blow flies are likely to be recorded as hosts (Sabrosky et al. 1989).

During a three-year study of interactions between *Protocalliphora* blow flies and Neotropical migratory bird species, bird nests were collected from study plots in Arkansas in the Ozark National Forest, in 1991, 1992, and 1993, and from the Ouachita National Forest in 1993. In Idaho, nests were collected during 1992 and 1993 from Targhee National Forest. Nests were located and monitored following the protocols detailed in Martin and Geupel (1993). When the nests were no longer active (i.e. after fledging, death, or depredation), they were collected in plastic bags, taken to the laboratory, and searched for *Protocalliphora* larvae and pupae. Larvae were collected from nestlings and fledglings whenever noted. The larvae and pupae were reared to maturity and identified using the taxonomic key provided

in Sabrosky et. al. (1989). Voucher specimens were deposited in the Univ. of Arkansas Museum of Entomology.

I recorded eight new host species for this parasitic genus of blow flies. In Arkansas, *P. deceptor* larvae were collected from Acadian Flycatcher (*Empidonax virescens*), Hooded Warbler (*Wilsonia citrina*), and Bachman's Sparrow (*Aimophila aestivalis*) nests. Larvae of *P. braueri* were collected from the nests of Black-and-white Warbler (*Mniotilta varia*) and Kentucky Warbler (*Oporornis formosus*). Subcutaneous larvae of *P. braueri* were collected from Kentucky Warbler nestlings and from a single Yellow-throated Vireo (*Vireo flavifrons*) fledgling. In Idaho, an unknown species of *Protocalliphora* larvae was collected from Veery (*Catharus fuscescens*) nests and *P. metallica* and an unknown *Protocalliphora* species from MacGillivray's Warbler (*Oporornis tolmiei*) nests. Unknown species could not be identified due to damage incurred during transport. These appear to be the first records of *Protocalliphora* parasitism in these bird species.

Acknowledgments.—I thank C. Sabrosky for identifying blow fly specimens. Numerous graduate students and field assistants collected nests in Arkansas and Idaho. J. Johnson and the University of Arkansas Cooperative Fish and Wildlife Research Unit provided transportation and laboratory space. T. Martin, L. Garner, S. Garner, and their field assistants collected nests in Idaho. A special thanks to N. Ball, S. Foster, R. King, and C. Sagers for thoughtful comments on earlier versions of this manuscript.

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Wilson Bull., 108(1), 1996, pp. 190–192

Observations of shorebird predation by snapping turtles in eastern Lake Ontario.—Accounts of snapping turtle (*Chelydra serpentina*) predation on birds other than waterfowl are rare. These include Laughing Gull (*Larus atricilla*) (Alexander 1921), Semipalmated Sandpiper (*Calidris pusilla*) and Lesser Yellowlegs (*Tringa flavipes*) (Street 1989), and the possible predation of a Forster's Tern (*Sterna forsteri*) chick (Fraser 1994).

The present observations were made at a freshwater dune ecosystem at the Nature Conservancy's El Dorado Beach Preserve in Jefferson County, New York. Thick, partially-submerged algal mats accumulate there annually in the shallow embayments of Lake Ontario. Large quantities of a green, filamentous algae (*Cladophora glomerata*) break off from underwater rocky substrates when the lake temperature exceeds 25°C, as in late summer (Vetterle 1976). The resulting offshore algal mats entrap invertebrates, including freshwater crustaceans, gastropods, and insects and some vertebrates such as small fish. This concen-

tration of food organisms is subject to predation by northern water snakes (*Nerodia sipedon*), painted turtles (*Chrysemys picta*), snapping turtles, and many species of birds, especially migrating shorebirds.

On 7 August 1994 at 16:15 EST, a Semipalmated Sandpiper was observed being pulled underwater, through an algal mat. The captured sandpiper was peeping loudly with only its head visible above water. The nearby shorebirds (Semipalmated Sandpipers and Lesser Yellowlegs) also vocalized excitedly. A Lesser Yellowlegs fluttered briefly above the site while vocalizing frenziedly. A large turtle's carapace was felt at the immediate location where the captured sandpiper was last observed; the turtle had presumably consumed the bird immediately. At 12:30 on 8 August 1994 another Semipalmated Sandpiper was pulled under the same algal mat by a snapping turtle. The bird was repeatedly pulled underwater, but resurfaced each time with its wings fully extended outward. This reaction made it difficult for the turtle to pull the bird through the algae. The event was photographed at the site. After I nudged the turtle's carapace with my foot, the turtle released the sandpiper. The bird quickly flew away, landed nearby, and began preening. The sandpiper shivered and preened for approximately 10 minutes, at which time it joined a close flock of feeding shorebirds. There was no visible damage to the bird.

At 12:25 on 11 August 1994 a large snapping turtle was observed crossing the sandy beach from an inland pond in order to enter the algal mat. The turtle was estimated to weigh between 10 and 15 kilograms, and had a carapace approximately 35 cm long. The shorebirds exhibited a distinct pattern of aggression in response to the fully exposed turtle. Three Black-bellied Plovers (*Pluvialis squatarola*) "escorted" the turtle closely. A Killdeer (*Charadrius vociferus*) stood further back and vocalized. Six Lesser Yellowlegs called and periodically fluttered in the air above the turtle. The remaining shorebirds (130–135 Semipalmated Sandpipers, four Sanderlings [*Calidris alba*], four Semipalmated Plovers [*Charadrius semipalmatus*], and one Spotted Sandpiper [*Actitus macularia*]) remained in a tight, distant group until the turtle was submerged under the algae. Within 15 min, the birds resumed normal feeding activity in the vicinity of the submerged turtle. It was later observed that there were two snapping turtles under the algal mat.

At 10:00 on 13 August 1994 a Lesser Yellowlegs was observed being pulled under the algae, with only its head exposed. Three other Lesser Yellowlegs were frantically peeping and fluttering above the victim. I again waded into the algae and nudged a large snapping turtle, which released the bird. The yellowlegs flew nearby, preened, and apparently had no damage done to its body or legs. It soon joined a feeding flock of shorebirds and could be identified by the algae and duckweed (*Lemna* sp.) remaining on its undertail coverts and legs.

It appears that individual snapping turtles can become efficient seasonal predators of shorebirds. Contrary to popular assumptions, even large snapping turtles did not rely entirely on strong jaw musculature to capture prey, but instead displayed a furtive hunting tactic. The delicate legs of those birds that escaped were not visibly damaged by the turtles' sharp, heavy mandibles, as might otherwise be expected. Populations of shorebirds, which may seem to be unlikely prey for sluggish snapping turtles, can be reduced during migration when feeding in areas where the turtles occur. Three confirmed events of snapping turtle predation on shorebirds, at the same site and within six days, represent a potential impact on migratory shorebird numbers.

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Erratum

The paper entitled "Gray Flycatcher predation on a hummingbird," in Wilson Bulletin 107:565–567, actually refers to observations of the Gray Kingbird. Although the correct scientific name is given, the substitution of "flycatcher" for "kingbird" escaped two referees, a proofreader, this editor, and (apparently) the author.

Wilson Bull., 108(1), 1996, pp. 193–204

ORNITHOLOGICAL LITERATURE

Edited by William E. Davis, Jr.

Arena Birds: Sexual Selection and Behavior. By Paul A. Johnsgard, illus. by the author. Smithsonian Institution Press, Washington, D.C. 1994: 330 pp., 38 color plates, 70 pen-and-ink illustrations. $39.95 (cloth).—Arena birds are those species that exhibit elaborate courtship behavior in well-defined, often communal areas called arenas. Familiar examples from North America include many of the grouse species, some duck species, as well as certain shorebirds such as the Pectoral (*Calidris melanotos*) and Buff-breasted (*Tringites subruficollis*) sandpipers. Familiar examples from outside of North America include the New Guinea and Australia birds-of-paradise and bowerbirds, the contingas and manakins of the Neotropics, and the European and African bustards. Other examples include species in such diverse groups as the parrots (the Kakapo [*Strigops habroptilus*] of New Zealand), the hummingbirds (the hermit species as well as others), African widowbirds and whydahs, and the Australian lyrebirds. Obviously, arena courtship has evolved independently in numerous taxonomically distant bird groups. It is one form of sexual selection, a pervasive evolutionary force in animals ranging from arthropods to apes. In this volume, Paul Johnsgard, known for his prolific popularized treatments of various of the world's bird families, has again attempted a broad review, this time not taxonomically oriented but evolutionarily oriented: arena courtship in birds.

Johnsgard's book is comprehensive and well referenced. It will prove important to students and researchers interested in sexual selection as manifested in arena courtship. A total of 460 references are included in the literature cited, making this volume clearly the best available review of this subject as it applies to birds. In addition, students will find the thorough 26 page glossary most helpful in that many definitions (Bateman's principle, handicap hypothesis, male dominance polygyny, sexy son hypothesis) are treated as short paragraphs, providing a very sound and quickly referenced summary of the complex terminology and conceptual hypotheses that currently pepper the field of sexual selection theory.

The book is divided into 12 chapters, most of which deal with specific taxonomic groups in which arena behavior is particularly dominant. The first two chapters are introductory, one to introduce sexual selection as an evolutionary process, the other to focus on arenas, courts, and leks. Both of these chapters try to provide a sound overview of relevant evolutionary theory, introducing (perhaps too briefly) the various models of sexual selection and the kinds of data sets that support sexual selection as an explanation for a particular courtship pattern. These chapters provide an adequate introduction to the field although they are best read after one has a relatively sound understanding of the principles of natural selection. Johnsgard gives perhaps an overly concise introduction to Darwin's thinking in conceiving of sexual selection (there is only a reference to "Descent of Man and Sexual Selection," none to "The Origin of Species," where the idea was first introduced) as well as to Alfred Russel Wallace's views on Darwin's theory. But one must remember that this is not a book on all of sexual selection but on only one form of it as shown in some birds.

There are seven tables in chapter 1 that will prove useful in gaining an overview of the numerous hypotheses that envelop this complex subject: models of sexual selection among birds, hypotheses that relate to male showiness among normally monogamous birds, hypotheses that relate to sexual monomorphism among nonmonogamous birds, costs and benefits influencing female mate choice strategies in lekking, costs and benefits influencing male clustering strategies, relative individual mating success among males of selected arena species, and examples of male age-related dominance/fitness ratios in lekking birds. Johnsgard's discussion is meant to summarize, although he does go into much greater depth when

discussing various species treated in the main body of the text. Chapter 2 is brief and also summary in nature. Johnsgard provides definitions of arenas, courts, and leks and attempts, as in the preceding chapter, to outline all of the relevant terminology in tabular form. Included in this chapter is a useful table listing all of the 60 arena bird species, describing for each its dispersion pattern (lek, exploded lek, mobile lek), color pattern (dimorphic, nondimorphic, reverse dimorphic), mass pattern (never clearly defined in the table but undoubtedly referring to males having greater, equal, or less mass than females), display types (aerial, ground, joint male, stage or arena, tree or shrub), and a principal reference source from the ornithological literature.

The remaining 10 chapters deal with specific examples. For example, chapter 9, "Manakins: spectacular soloists and dazzling duets," spotlights the 24 species of lekking Neotropical manakins, some of which have been intensively studied and for which much is therefore known. Even readers quite familiar with this group will find Johnsgard's treatment praiseworthy. He discusses well-chosen examples, provides excellent pen-and-ink diagrams of the behaviors he describes (a very useful feature throughout the book), and summarizes the essential hypotheses that have been advanced to account for the elaborate behaviors. Other chapters are similar in approach.

What is missing from the volume is a final chapter that insightfully brings together the numerous threads contained within the main body of the text. There is no concluding chapter of any kind. Missing, therefore, are comparisons among taxonomically distant groups, substantive discussions of convergent evolution, and suggestions about how such diverse taxa evolved independently into arena birds. There is, for instance, no real comparison of the ecology of Neotropical species such as the Guianan Cock-of-the Rock (*Rupicola rupicola*) with that of the various species of New Guinea birds-of-paradise, two cases in which a frugivorous diet has been suggested as influential in structuring the birds' reproductive ecologies. This quibble aside, anyone interested in this subject cannot but help to find Johnsgard's book of great use. It is a most thorough popular review of the literature, greatly enhanced by numerous well-crafted illustrations.—John C. Kricher.

My Double Life: Memoirs of a Naturalist. By Frances Hamerstrom. University of Wisconsin Press, Madison. 1994: 316 pp., 72 black-and-white photographs, 42 line drawings. $16.95 (paper); $35 (cloth).—This autobiographical sketch consists of 90 snippets—recollections and reminiscences—mostly two-to-four pages in length, which provide a window into the life of an accomplished naturalist and conservationist. The first 85 pages or so deal with Frances's childhood—glimpses into the secret life of a bright, alert, questioning, secretive, naughty, awful, and sometimes manipulative child—the kind that drives parents and governesses to distraction but often produces accomplished adults. The descriptions, for example, of a child of six smoking cigarettes, cutting her new Christmas doll's hair, conducting a formal funeral for a Blue Jay, or cutting up her mother's white kid opera gloves to make jesses for her pet kestrel, are sometimes sad, sometimes humorous, sometimes poignant. There are undertones of strife against grownups who "forbade wild pets and tried to squelch my companionship with creepy crawly creatures . . ." She found grownups "either weak or not to be trusted." Another 20 pages deal with the metamorphosis of a tomboy into a young woman.

The remainder of the book deals largely with the prairie chicken work she shared with her husband of 59 years, Frederick, with occasional glimpses and hints of raptor research. We follow their lives in a series of deserted farmhouses in central Wisconsin during the Great Depression and war years—behavioral studies from blinds, harsh winters with frozen

pumps and prairie chicken censuses on snowshoes, graduate school with Aldo Leopold, a succession of 7000 "boomers," or helpers, with the chicken work, parenting under primitive conditions (two children), and local politics and conservation initiatives.

This book is well written, well illustrated, and provides an interesting perspective on some facets of ornithological research, particularly during the first half of the twentieth century. What were the two lives of this most interesting ornithologist/naturalist? Read this delightful book and find out for yourself—I highly recommend it.—William E. Davis, Jr.

Annotated Bibliography of the Loons, Gaviidae. By Judith W. McIntyre and Norma G. Cutler. North American Loon Fund, Gilford, New Hampshire. 1995: 170 pp. Available in paperback for $12 plus $2 S&H within U. S. A. from: NALF, 6 Lilypond Road, Gilford, NH 03246.—This bibliography contains 1650 citations with the most recent 1994. The introduction lists 44 sub-categories (e.g., acid rain, food, predation) for which separate sub-bibliographies may be obtained. Anyone purchasing the entire bibliography is entitled to one free sub-bibliography, and additional ones at cost, ordered from the above address. Not available on disk. About half of the entries are annotated, and annotations run up to nine lines of type. This bibliography will be useful for anyone interested in loon biology or conservation.—William E. Davis, Jr.

Atlas of the Breeding Birds of New Hampshire. By Carol R. Foss (ed.). Audubon Society of New Hampshire, Dover N. H. 1994. 459 pp., many b/w sketches, 241 maps. $39.95 (cloth).—This publication from a New England state continues the expansion of the breeding bird atlas shelf in libraries. The birders of the Granite State have produced a fine work which matches the high standards of the earlier Atlases.

The book follows the well-known format, with a page of text and a sketch of the species facing a map occupying a full page. The resulting large maps for a small state are perhaps the most easily interpreted of any in the atlases I have seen. The atlas blocks were set up on the standard 6 blocks per 7.5 minute topographic sheet, but as with several other states having limited manpower only one block per sheet was selected as a "priority block."

New Hampshire has varied habitat and the second greatest altitudinal range of any eastern state (from sea level to over 6200 feet.) This variety has been organized under 16 physical divisions. The Atlas workers found breeding evidence for 204 species with 176 of these "Confirmed". Twenty-one other species are listed as "Historically or potentially breeding" species which were not found during the atlas project. No attempt is made to consider populations using Breeding Bird Survey data or something similar as other state atlases have done.

The species accounts, written by a large panel of experts, provide a variety of natural history information, some it from New Hampshire publications but much of it from standard sources such as the Bent series. Besides the customary table summarizing the number of blocks for which "Confirmed", "Probable", and "Possible" status was obtained for the species, another table detailing the number of records meeting each of the criteria for confirmation (i.e., Nest Building, Nest with eggs, etc.) together with the range of dates for each. This useful information is not included in other atlases.

Besides the species accounts and the usual summary of the geography of the state, there are two essays that are unique for this atlas. A chapter entitled "Major Changes in Breeding Avifauna of New Hampshire Since Its First Settlements by Europeans in 1623" gives a

very lucid historical discussion of the effect of settlement and habitat change, as well as more recent range changes. Accompanying this is an appendix showing range maps for the period 1963–1980 of several species. Some of these have greatly disappeared in this short interval. Another fascinating chapter by Tudor Richards is a discussion of the occurrence of species along the great altitudinal gradient in the state. Richards attempted to count the species present at 500 foot intervals at stations throughout the state. He classifys his results results into seven avifaunal regions. The highest count was 134 species in the interval between 1000 and 1500 feet, and the lowest count was one species (Dark-eyed Junco) in the 5500–6000 feet interval.

I have only one minor negative comment. The maps of land elevations and forest types are done in a 6-interval "gray" scale. It is next to impossible to distinguish between the three darkest categories.

The field work for this atlas was completed in 1986, and the long delay in publication seems to be characteristic of the atlas business. Other states have experienced similar delays. In any event, this is a well-done compilation and welcome addition.—George A. Hall.

A Birder's Guide to Coastal North Carolina. By John O. Fussell III. Univ. of North Carolina Press, Chapel Hill. 1994: 540 pp., 10 black-and-white photographs, 44 maps. $16.95 (paper); $29.95 (cloth).—The purpose of this book is to describe and facilitate visiting the better birding sites along the North Carolina coast. It accomplishes this goal in fine fashion. The book is divided into three parts. Part 1 consists of three chapters, the first of which describes the climate, physiography, and habitat of the various sections of the coast. The second chapter provides general planning and travel advice and introduces birders to the pleasantries of ticks, fire ants, and poisonous snakes. Chapter 3 is a list of more than 350 species which may be found in the region, with annotations on status, season, and habitat and sometimes specific site information of from one to nine lines of text; a list of 41 accidentals is included. Part 2 is a site guide consisting of six chapters, five of which describe (from north to south) sections of the coast and associated "tidewater" or outer coastal plain. The sixth deals with pelagic birding. Each chapter has a map of the entire section of coast described, and detailed maps for particularly interesting sites. There is usually a section on logistics, and the text guides the reader on a "tour" of each site with distances described to the nearest tenth of a mile, notable birds enumerated, and habitats described. Telephone numbers, e.g., for pertinent wildlife refuge headquarters, are included, as are helpful hints about avoiding problems with hunting seasons. The text is highlighted by ample, common sense advice. For the site I had most recently visited (fall 1994), I found the directions and descriptions excellent; I assume that this is the rule rather than the exception. Certainly, the text reads smoothly and the directions are clear and detailed. Part 3 consists of more detailed descriptions of status, season, distribution, habitat, and special features of 141 bird species "of special interest." The accounts average a third to half a page, but some run to two pages. An appendix contains detailed bar graphs describing seasonal occurrence and status (common, rare, etc.) of all but accidental species. The graphs are large, detailed, and user friendly, with a status key on each pair of facing pages.

The book is generally well done, but is not without problems. It is a big book—it won't fit in your pocket or in most automobile glove boxes. This large size at least partially results from redundancy (which the author acknowledges) among the annotated bird list (chapter 3), the section on birds of special interest (part 3), and the bar graphs—triple coverage for 141 species. Integrating the annotated lists would probably have been a good idea. Nowhere in the book is there a map of the entire region to help a reader unfamiliar with the region

put into a visual context the physiography and habitat descriptions in the opening chapter. But despite these few detracting features, I would recommend the book and consider it indispensable for anyone planning to visit the North Carolina coast.—William E. Davis, Jr.

The Birds of Kentucky. By Burt L. Monroe, Jr. Indiana Univ. Press, Bloomington, Indiana. 1994: 145 pp., numerous color plates. $49.95.—"The birds of Kentucky" is an attractive "coffee table" book describing all birds known to have occurred in that state. The late author was the dean of Kentucky ornithologists and one of the grand men of our science. However, anyone looking for new or comprehensive information about the birds of Kentucky will be disappointed by this book. Why such beautiful tomes are done with such thin detail continues to bewilder me. On the other hand, the illustrations in the book are outstanding. William Zimmerman is one of the best illustrators of living birds in the world and the figures in this book demonstrate his abilities. It is unfortunate that not all species were illustrated. The reference section is comprehensive and well done. I wish the rest of the book was as thorough in its coverage.—C. R. Blem.

The Chronicles of the Rowleys. By Peter Rowley. Huntingdonshire Local History Society, Huntingdon, Cambridgeshire, England. 1995: 158 pp. Available in U.S.A. from Peter Rowley, 815 Park Avenue, New York, New York 10021. $25 (cloth).—This book provides glimpses of English life for about a century (ca 1780–1880) from the perspective of one family, the Rowleys. People with such phonic names as Owsley Rowley stride across the stage of English history. All of the chapters should be of interest to those with a general fascination for history, but one chapter, "The Rigid Squire and the Eclectic Ornithologist" (25 pages), is a biographical account of ornithologist Dawson Rowley (1822–1878). Dawson, under the influence of famed ornithologist Alfred Newton, compiled two massive volumes on the Great Auk (*Pinguinus impennis*) which, although never published, are apparently still extant. After Rowley abandoned the Great Auk project, he turned his attention to the publication of three volumes of *Ornithological Miscellany*, published in parts as a magazine beginning in 1875 and before his death in 1878. These issues apparently included hand-colored lithograph plates by John Gerard Keulemans.

The book is a scholarly work based on primary sources (mostly correspondence) and should appeal to those interested in the history of ornithology.—William E. Davis, Jr.

Before the Echo: Essays on Nature. By Pete Dunne. Univ. Of Texas Press, Austin. 1995: 152 pp., 20 line drawings. $19.95 (cloth).—In contrast to his previous books of essays, which dealt mostly with birds, this collection of 30 essays deals largely with other facets of the natural world. Most of the essays were first published in the New Jersey edition of the Sunday New York Times. The essays treat a variety of rather mundane subjects, such as the first snowfall of the year, confrontations with mice in an old farmhouse, or burning leaves in the fall. My favorite, "Before the Echo," deals with hunting, and is not a polemical anti-hunting statement but rather a consideration of hunting as a natural phenomenon. Many of the essays center on poignant reminisces of youth (e.g., catching fireflies), and most have a mildly polemical, but not offensive tone (after all, Pete Dunne is an environmentalist who has worked most of his professional life with the New Jersey Audubon Society). He does go after an occasional Sacred Cow, such as the grass lawns of suburbia.

Pete Dunne has become one of the premier natural history writers of North America, and his essays are beautifully written. You may not always agree with his biases, but the stories he tells and the yarns he spins are delightful. Even though there isn't much about birds, I would recommend reading this book to anyone interested in the interaction of people with the natural world.—William E. Davis, Jr.

Birds of the Cayman Islands. Revised edition. By Patricia Bradley, photography by Yves-Jacques Rey-Millet. Caerulea Press, Italy. 1995: 261 pp., 77 color photos, 4 maps. No price given (cloth).—This excellent little guide has been substantially revised, and the status of individual bird species updated, with several new species added and the status of many changed. The photographs are much the same as in the first edition (1985), but there have been a few replacements and the number of habitat photos increased. In the copies I examined, the new edition photos were not as sharp as those of the first edition, but the color seemed to be more realistic, at least in some photographs. The maps have been redrafted and updated, and the bibliography has been considerably expanded. A new appendix provides a check-list of breeding birds with status and distribution for each of the three islands. Most of the minor errors mentioned by Jon Barlow in his thorough review of the first edition in *The Wilson Bulletin* (1987, 99:512–514) seem to have been corrected, although curiously, the subspecific designation *bairdi* for the local Jamaican Oriole (*Icterus leucopteryx*) is still misspelled.

This book should be indispensable to anyone visiting the Cayman Islands and remains an important component of Caribbean ornithological literature.—William E. Davis, Jr.

Swifts. By Phil Chantler and Gerald Driessens. Pica Press, East Sussex, U.K. 1995:237 pp. £ 26.—This field guide is similar to others on seabirds, waterfowl, sparrows, warblers, and shorebirds published by Houghton-Mifflin and Princeton Univ. Press. As such, this volume becomes an important addition to the library of those interested in knowing and identifying the birds of the world. The present book carries on the tradition of the others in that it is considerably more than just a field guide. The book contains a rich variety of information about swifts. It provides maps of the distribution of the swifts of the world, gives detailed descriptions of status, relative abundance, migration, breeding, adverse factors, habits and habitat, and describes problems of identification. I greatly enjoyed the sections on swift biology, the possibility of new (undescribed) species, conservation, and "how to watch swifts." The reference section is comprehensive and modern. The binding and format are excellent and the book is attractive.—C. R. Blem.

Contributions to the History of North American Ornithology. William E. Davis, Jr. and Jerome A. Jackson (eds.). Memoirs Nuttall Ornithol. Club. No. 12. Cambridge MA. 1995: vii +501 pp., many b/w photos. $40 (cloth)—This book is an outgrowth of a symposium on the history of North American ornithology given at the 1991 meeting of the Association of Field Ornithologists. The editors gathered the material of that symposium together with a number of invited chapters into an engaging and valuable preamble to a definitive history. The history of American ornithology is a neglected subject, and many current workers show a lack of interest in it, possibly because they lack any knowledge of

it. A history was contemplated as a part of the Centennial celebration of the AOU but this did not eventuate.

The bulk of the book consists of 11 chapters detailing the development of ornithology at as many noted centers of ornithological research: 7 museums and 4 universities (also with museums.) Since the authors of these accounts are usually noted and important participants in their subject institutions, the result is a set of fascinating stories. Thus we have the Academy of Natural Sciences of Philadelphia (by Gill); U.S. National Museum of Natural History (Banks); Harvard's Museum of Comparative Zoology (Barrow); Univ. of Kansas (R. Johnston); American Museum of Natural History (W. Lanyon); Field Museum (Lowther); Carnegie Museum of Natural History (Parkes); Univ. of California's Museum of Vertebrate Zoology (Johnson); Cornell Univ. (Butcher and McGowan); National Museum of Canada (Ouellet); and the Royal Ontario Museum (Barlow).

The format and content of these chapters varies from institution to institution. Some are straightforward historical summaries, but some include delightful anecdotes about people whom we all know by reputation, but who have lived before our time. Most of the accounts detail the major contributions of the institution, and some itemize the strength of their collections. The MVZ account contains a series of short biographies of many of the people associated with that museum, and also includes an "academic genealogy" of Joseph Grinnell involving a list 50 distinguished present-day ornithologists who are "academic grandchildren". The Cornell and Kansas Universities each has a list of the doctoral degrees granted in ornithology. The problems of the present day come into view in Henri Ouellet's low keyed description of the regrettable situation at the Canadian National Museum.

Most of the accounts are illustrated by excellent photographs. These range from formal studio shots, through group photos of departmental staffs, to informal shots in the field, highlighted by one of a group from the MVZ taking a bath in a Mexican stock tank at the end of an expedition. One impressive group photo taken in 1984 shows 40 people associated with the University of Kansas. I was most interested to see photos of Annie Alexander, C. E. Hellmayr, J. T. Zimmer, and Witmer Stone. (If the reader cannot identify these people, he will learn much from reading this book.) It is also interesting to see youthful photos of some of the "Elders of Our Clan", whom we perhaps knew only in their declining years.

In addition to these chapters there is a chapter on ornithological research within the U.S. Forest Service (by R. Conner) and one on the history of Canadian ornithology (by M. G. Ainley).

The three final chapters are more general. Edward Burtt and Alan Peterson discuss "Alexander Wilson and the Founding of North American Ornithology." Besides a brief outline of Wilson's life there is a detailed discussion of Wilson's contribution to the taxonomy of North American birds. Wilson claimed to have first described 51 species, but the AOU Check-list today gives him credit for only 20. Burtt and Peterson provide a table correlating Wilson's taxonomy with that of the present day. The authors then discuss in turn their ideas of Wilson's contributions to aspects of ornithology unrelated to taxonomy, his contributions to nature writing, and his influence on bird illustration.

In a chapter derived from a paper given at the 1990 WOS meeting François Vuilleumier and Allison V. Andors describe the "Origin and Development of North American Avian Biogeography." They argue convincingly that this history is a good example of Kuhn's "paradigm" model of scientific progress.

The final chapter by Davis and Jackson is an annotated listing of "The Literature of the History of North American Ornithology." About 300 references are discussed in a classified fashion, in which they hope to guide to researchers interested in the history.

In summary, this is an excellent beginning. I recommend it to all with no reservations. It may be a selfish thought to want more of a good thing, but I for one do. The reader can

think of several institutions (perhaps his own) which are not included. Other subfields of ornithology could profit by having historical reviews done. The present editors hint that they might prepare a second volume. Indeed, Dr. Jackson has hinted to me that they might eventually attempt a full scale history. Let us hope that they do.—George A. Hall.

A Naturalist in Indian Territory: The Journals of S. W. Woodhouse, 1849–50. Edited and annotated by John S. Tomer and Michael J. Brodhead. University of Oklahoma Press, Norman, Oklahoma. 1992: 304 pp., 26 figs., 4 maps. $29.95 (cloth).—In 1849 and 1850—over two decades after the Creeks had been forcibly resettled into Indian Territory (now the state of Oklahoma)—the Corps of Topographical Engineers finally surveyed the northern and western boundary of their new homeland. The individual selected to serve as surgeon-naturalist for the expedition was Samuel Washington Woodhouse (1821–1904), an assistant resident physician at the Philadelphia Hospital. Woodhouse had first become interested in natural history as a teenager. Soon he discovered the Academy of Natural Sciences of Philadelphia, where he spent long hours pouring through the specimen collections, interacting with some of the leading naturalists of his day, and learning the rudiments of ornithological theory and practice. A lack of employment prospects prevented the young man from seriously considering the idea of ornithology as a vocation. Instead, Woodhouse decided to pursue the more traditional careers of farming and medicine. However, he did not completely lose his taste for natural history, and when the opportunity to join the Creek boundary survey presented itself, the single, twenty-seven-year-old doctor quickly seized it.

By the mid-nineteenth century, the Creek Nation contained numerous scattered settlements, and Woodhouse was the first naturalist to undertake a systematic scientific inventory of the area. The expedition's slow pace and relatively light medical caseload allowed him ample time to examine the flora and fauna of the region. After two seasons in the field, Woodhouse brought back over two thousand specimens, including 15 animal forms which proved new to science. Among these were a new kind of Mourning Dove (*Ectopistes marginella* Woodhouse, now *Zenaida macroura marginella*). In 1849, Woodhouse also collected the skin of the previously undescribed Prairie Falcon (*Falco mexicanus*), but he failed to gain credit for the discovery because he carelessly mistook the specimen for a Peregrine Falcon (*F. peregrinus*). One year later, before anyone caught the mistake, the German ornithologist Hermann Schlegel named and described the Prairie Falcon based on another specimen taken in Nuevo León, Mexico. The editors of the volume at hand were able to track down this and many other interesting episodes associated with the expedition by examining surviving specimens at the Academy of Natural Sciences of Philadelphia, the National Museum of Natural History, the Museum of Comparative Zoology, and other natural history repositories.

In addition to many valuable specimens, Woodhouse also brought back three private journals which Tomer and Brodhead have carefully edited for publication. These documents contain fascinating descriptions of the survey party's experiences in the field, detailed accounts of medical practice on the frontier, as well as invaluable observations about the environment and people of the Creek Nation in the mid-nineteenth century. A lengthy introduction and careful annotations help to illuminate and place into broader context Woodhouse's sometimes cryptic entries. Included in the introduction are a thorough (though occasionally tedious) summary of early western exploring expeditions, a brief history of the Creek boundary expedition, an examination of the significance of Woodhouse's natural history work in Indian Territory, and a sketch of his life. The annotations run the gamut from discussion of current scientific names of plants and animals mentioned in the text to

identification of the people, places, and objects Woodhouse encountered on his journey. Tomer and Brodhead have done an excellent job of making these important journals accessible to a broad audience, although this reader would like to have seen a few more of Woodhouse's fine field sketches reproduced.

Shortly after his return from Indian Territory, Woodhouse returned to the field as a member of the Zuni and Colorado rivers expedition (1851–1852) and a private expedition to Central America (1853). For reasons that are still unclear, he devoted the remainder of his life to professional medical practice. Although his collections and publications were significant, they were soon overshadowed by the work of the well-funded and highly publicized Pacific Railroad Surveys of the 1850s. Woodhouse and his scientific contribution faded into obscurity. Tomer and Brodhead have done a great service in resurrecting the legacy of this important but forgotten naturalist.—Mark V. Barrow, Jr.

The Eastern Screech-Owl: Life History, Ecology and Behavior in the Suburbs and Countryside. By Frederick R. Gehlbach, Texas A & M Univ. Press, College Station, Texas. 1994: 302 pp., a color frontispiece with no caption, ten chapters, 34 black-and-white photographs, 27 tables, 25 figs., $45.00 (hardcover).—This book is a personal narrative of 25 years of Gehlbach's studies of Eastern Screech-Owls (*Otus asio*) in central Texas. For eleven of those years (1976 to 1987), Gehlbach compared the life history of suburban and rural populations. Gehlbach's passion for these owls and for natural history in general surfaces throughout the book.

In chapter one—"On Studying Screech Owls," Gehlbach outlines the beginnings of what he terms the exploratory (1967 to 1975), or trial and error period, and the confirmatory period (1976 to 1991). There is also a brief overview of statistical procedures. Chapter two—"Landscapes," a straight forward description of the suburban and rural habitats—vegetation, nesting and roosting environments. Chapter three—"Food Supplies and Predation." Food niche, prey species, seasonality, and prey body mass are all calculated from cached prey, but no pellet analysis was conducted. Gehlbach provides data on hunting tactics and periodicity from direct observations. The brief discussion on mobbing is interesting, as Gehlbach convincingly correlates resident mobbers with their potential as prey. Chapter four—"Adult Weight, Coloration and Molt." Comparative weights of 80 males and 166 females provide ample samples for some of Gehlbach's analysis. In particular, the weight dynamics seem to be tied to weather and food fluctuations. There is a lengthy discussion on red and grey color morphs and speculation as to why. The molt data, although brief, seems adequately covered. Chapter five—"Eggs and Incubation." This chapter chronicles the start of the nesting season from egg laying and replacement clutches through clutch and egg sizes, laying intervals, incubation duration, and hatching. Of particular note, is the re-mating and re-laying by one female whose mate was killed by a car while she incubated one egg. She abandoned the egg after six days, re-mated three days later and re-nested about 12 days after that. Chapter six—"Chicks and Fledglings." In his longest chapter, Gehlbach uses male roosting proximity to nests as a barometer of egg hatching, brooding and fledgling. Hatch dates, sequences, brooding, nest microclimate, parental responsibility, growth rates, mortality, nest-cavity symbiosis, fledging and dispersal are all well covered. Two bits of information I found particularly interesting were; (1) "coincidental hatching" in which the typical asynchronous hatching of most owls was complicated by the fact that 13 (23.6%) and eight (14.5%) of 55 clutches, respectively, had two and three eggs respectively hatch within a 24 hour period (p. 105); and (2) "nest-cavity symbiosis", in which Eastern Screech-Owls bring live Texas blind

snakes (*Leptotyphlops dulcis*) back to the nest cavity and these snakes apparently eat insects that might compete with nestlings for stored food items. In fact, young in nests with these snakes grew faster and had better survival than nests without them. Gehlbach concludes this is probably coincidental and not selective. In any case it is very intriguing. Chapter seven—"Vocalizations." An overview of song types, hoots, barks, non-vocal sounds, and juvenile development is given. Gehlbach describes in which context and chronology the various sounds are produced. This perhaps is the weakest chapter. Chapter eight—"Lifetime Reproduction." Discussions on age and size, nest sites, mates, recruitment, and inheritance are provided. Most of the data, however emphasizes females because sample sizes were to small for males. Gehlbach summarizes this chapter by stating that about half the females each season are yearlings, of which about half disappear after their first attempt at breeding. Those yearlings that reproduce successfully are usually larger and tend to show site fidelity in following years. Life long monogamous pair bonds are the general rule, with few polygynous relationships. Interestingly, females began to have smaller clutches and fledged fewer young after about age five. Chapter nine—"Population Structure and Flux." Topics include age classes and survival, productivity, use of space, densities and cycles. This is a good overview of Gehlbach's marked individuals and comparative data between the suburban and rural populations are given. Survival is better in the suburbs, but surprisingly these owls have short life spans, except in a few cases. Breeding densities seemed to fluctuate in relation to environmental factors and predators, and Gehlbach concludes that the suburban owls exhibit a nine year cycle, similar to the 9.3 year lunar cycle. Chapter ten—"The Suburban Advantage." Gehlbach sums up the advantages that his suburban screech owls have over rural screech owls. The sections are pre-adaptations of Eastern Screech-Owls, connections, and prescriptions for the future.

Throughout the entire book, Gehlbach has carefully compared many aspects of these owl's life history. In short, the suburban birds seem to have an easier life than the rural birds. Whether this is really important for the screech-owl population of central Texas is for the reader to decide. In any case, this small owl seems well-adapted to a wide range of habitats and habitat modification due to people.

Although it appears that the book was intended to be readable for all audiences interested in natural history, it is not. It is a technical book. The book is beyond the interest of average bird watchers or naturalists. Even the serious researcher must review each page carefully to fully understand the message. Gehlbach's continuous emphasis throughout the text concerning the exploratory period gets a bit old. I agree that it often takes a few years to become familiar with the organism one is studying, but I believe that an eight-year exploratory period is not necessary. I also would have liked to see more reference to Van Camp and Henny (1975, The screech owl: its life history and population ecology in northern Ohio. North American Fauna 71). This was also a long-term study that could have provided a lot of comparative data to Gehlbach's work. Gary Ritchison and his graduate students have also published a number of good papers on Eastern Screech-Owl vocalizations and dispersal in Kentucky, but deserved more recognition. Perhaps less comparisons with Boreal Owls (*Aegolius funereus*) and more with other species of *Otus* also would have been preferable.

Should you buy this book? Absolutely. There is an incredible amount of information throughout the book. I recommend this book for anyone studying birds. Gehlbach's 25 years of screech-owl watching have given him much time to think of various ways to analyze data. There are many good ideas for other species. Although one may not agree with his methods or conclusions, these types of long-term data are rare. Although the book at $45.00 is expensive, it has a hard cover, includes a great deal of information and will last a long time—buy it!—DENVER W. HOLT.

THE BIRDS OF NIGERIA. By J. H. Elgood et al. British Ornithologists' Union Check-list No. 4 (second edition). 1994. 306 pp., hardback, 7 figs., 10 tables, gazetteer, 16 color plates of habitat and 48 of Nigerian birds. £21.00 (UK), £23.00 (overseas) including postage from British Ornithologists' Union, % The Natural History Museum, Akeman Street, Tring, Herts. HP23 6AP, UK.—Nigeria is among the ten most populous nations on earth, with a size and human density comparable to that of Pakistan. It is hardly a premier destination either for ecotourists or ornithologists. In 1976, the British Ornithologists' Union began to publish check-lists of avifaunas for little-known countries and regions of the world. "The Birds of Nigeria" first appeared in 1981, compiled by J. H. Elgood, a former professor of zoology (1949 to 1965) at Ibadan University in that West African nation, who described the country's only endemic bird species, the Ibadan Malimbe (*Malimbus ibadanensis*). When the first edition of "The Birds of Nigeria" sold out ten years after publication, the B.O.U. prevailed upon its author to spearhead its revision and updating, which happily appeared in his 85th year.

As a national check-list, this work is exemplary. Not only does it contain an annotated list of about 900 species reported in the country to date (884 being admitted to the official list), but it also has excellent summaries of Nigeria's environment—its topography, geology, climate, weather, and vegetative zones. Migration and breeding both are insightfully categorized and summarized. It has a list of names of people who have recorded birds in the country, several maps plus an excellent gazetteer, a compilation of banding recoveries (none intra-African), and a comprehensive bibliography. In short, I found everything one might hope for in a work of this nature.

The color photos, including an attractive cover photo of a Red-throated Bee-eater (*Merops bullocki*), plus a lovely color painting of the endemic Ibadan Malimbe by Martin Woodcock, all are welcome enhancements to this second edition. Other changes since the first edition, in addition to adding and updating species accounts and various summaries, include the renaming and reordering of the avifauna to conform largely to "The Birds of Africa" series ("*BoA*", Academic Press 1982 ff). Appendices list the numerous changes to both scientific and English names between editions. *BoA* was a sensible choice for a taxonomic and nomenclatural model, but unfortunately it is not yet complete; the four volumes published to date cover only slightly more than 60% of Nigeria's species. Elgood and his team had access to some *BoA* work in progress, but for species towards the end of the systematic order, parts of the original nomenclature, including such quirky English names as Exclamatory Paradise Whydah (*Vidua interjecta*), can be found. It might have been better to have followed the well-researched taxonomy and nomenclature of Dowsett and Forbes-Watson's "Checklist of Birds of the Afrotropical and Malagasy Regions," Vol. 1 (Tauraco Press 1993), cited in the bibliography, for the remaining species.

If there is any overall problem with this work, it involves the authors' difficulty in restating the present status of Nigeria's birds after considering the massive changes in the Nigerian environment since Elgood left the country some thirty years ago. Much of the book is based on data gathered by him and several essentially contemporaneous expatriates, updated whenever possible by more recent material. Sadly, the latter is at best spotty. Details of evidence (existence and location of cataloged specimens, photographs, sight report documentation, etc.) to support many species' stated status also would have enhanced the checklist's authority. A more conservative assessment might have admitted somewhat fewer species to the official list, and more current information if available might have decreased the stated distribution and abundance of many species. In relation to this work's overall usefulness, however, these comments are minor.

When asked to update his original section on Nigerian vegetation, Ronald Keay revisited the country and reported wryly, "There is no vegetation left in Nigeria!" With most local

biological work to date having been undertaken by foreigners, the importance of a work such as "The Birds of Nigeria" cannot be understated. It perhaps was not coincidental that the Nigerian Conservation Foundation (NCF) was formed locally shortly after the first edition was published. The NCF has been instrumental in establishing the framework for sound national conservation policy. This second edition gives a concise statement of the present conservation situation. One can hope that now expanded, improved, and more attractive, this new edition will inspire more direct local interest in the country's birds and their protection.

B.O.U.'s support of basic efforts like compiling check-lists worldwide may have more ultimate impact on protecting the earth's birdlife than any other modest single measure I can think of. I salute both the B.O.U. and the authors of "The Birds of Nigeria," as should we all. At less than $40 in hardback, this book is a worthwhile bargain for any student of West African avifaunas. Its purchase also further encourages the B.O.U. to continue its fine program.—P. William Smith

ADDENDUM TO "BIRDS OF CONIFEROUS FOREST ON MOUNT GRAHAM, ARIZONA," Wilson Bulletin 107(4):719–722

Audio evidence recorded by the author, Joe T. Marshall, and engineered by Michael A. Wascher, is available gratis as a 66-min stereo recording to accompany this article. The 17 tracks are arranged from lower to higher elevations along Swift Trail, Mount Graham. Besides nearby birds, other species heard in the background at each altitudinal station are listed in an accompanying printout. Send written or electronic mail requests stating your scientific or other interests in Mt. Graham birds to Joe T. Marshall, National Museum of Natural History, Room 378, Washington, D.C. 20560-0111 (email: mnhvz113@sivm.si.edu). Indicate whether your preference is to borrow a digital audiocassette, borrow a CD, or receive one of a limited supply of analog audiocassettes.

This issue of *The Wilson Bulletin* was published on 1 March 1996.

The Wilson Bulletin

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Suggestions to Authors

See Wilson Bulletin, 107:574–575, 1995 for more detailed "Information for Authors."

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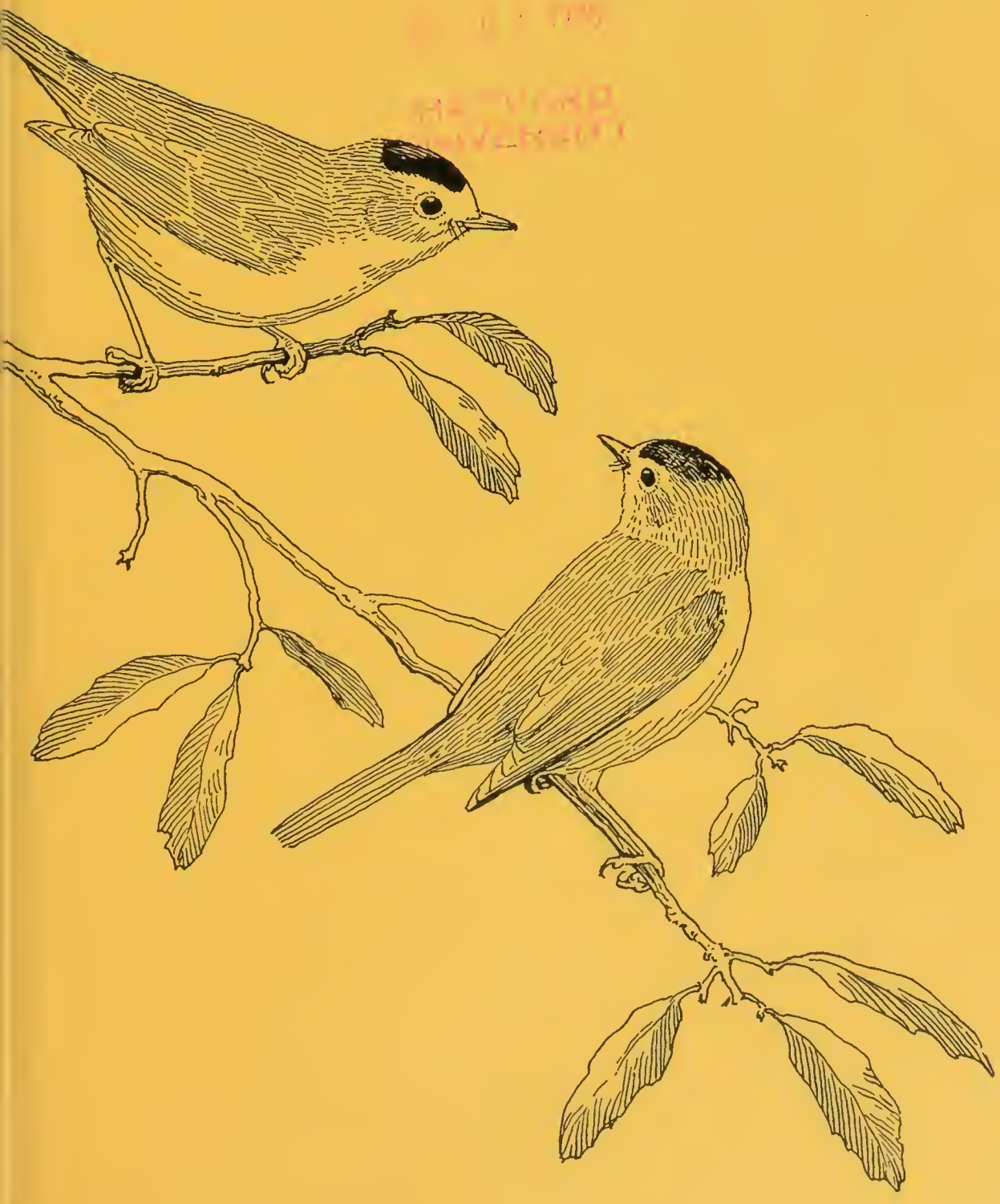
The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 108, NO. 2 JUNE 1996 PAGES 205–396

(ISSN 0043-5643)



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THE WILSON BULLETIN
(ISSN 0043-5643)

THE WILSON BULLETIN (ISSN 0043-5643) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th Street, Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Second-class postage paid at Lawrence, KS. POSTMASTER: Send address changes to THE WILSON BULLETIN, P.O. Box 1897, Lawrence, KS 66044-8897.

Back issues or single copies are available for $12.00 each. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

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Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

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THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Society

VOL. 108, NO. 2 JUNE 1996 PAGES 205–396

Wilson Bull., 108(2), 1996, pp. 205–227

GEOGRAPHIC VARIATION AND SPECIES LIMITS IN *CINNYCERTHIA* WRENS OF THE ANDES

ROBB T. BRUMFIELD[1,2] AND J. V. REMSEN, JR.[1]

ABSTRACT.—Few studies have quantified geographic variation in widely distributed Andean birds despite the fact that the linearity of their distributions provides unique opportunity to assess latitudinal geographic variation. We examined geographic variation of morphometric and plumage characters in populations currently treated as a single species, the Sepia-brown Wren (*Cinnycerthia peruana*), that inhabits humid montane forests from northern Colombia to central Bolivia. Our analysis supports the recognition of three biological species (*olivascens, peruana,* and *fulva*) based on discrete morphometric differences as well as marked plumage differences. Size variation within populations is inconsistent with the predictions of Bergmann's Rule, whereas variation across species runs counter to the predictions, with the smallest species occurring farthest from the Equator. *Received 20 June 1995, accepted 10 Dec. 1995.*

Before hypotheses concerning the origin and maintenance of geographic variation in bird species can be formulated, the patterns of variation must be well-described (Zink and Remsen 1986). Although the humid slopes of the Andes mountains are potentially one of the world's most productive areas for the study of geographic variation (Remsen 1984a, Graves 1985, 1988), few workers (e.g., Graves 1982, 1985, 1991, Remsen et al. 1991) have quantified geographic variation in widely distributed Andean birds. We present here an evaluation of morphometric and plumage variation in populations currently treated as a single species, the Sepia-brown Wren (*Cinnycerthia peruana*), that inhabits humid montane forests in the temperate and subtropical zones of the Andes from northern Colombia to central Bolivia (Fig. 1). We also re-evaluate species limits among these populations.

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COLOMBIA
ECUADOR
BOLIVIA
PERU

The four currently recognized subspecies of *Cinnycerthia peruana* (*bogotensis, olivascens, peruana,* and *fulva*; Paynter 1960, Ridgely and Tudor 1989, Fjeldså and Krabbe 1990) were all originally described as distinct species based on size and plumage differences. Known only from the eastern Andes of Colombia, *bogotensis* differs from its geographically closest relative from the rest of the northern Andes, *olivascens,* by its darker coloration (Hellmayr 1934, Fjeldså and Krabbe 1990). Nominate *peruana* is smaller in size and less olivaceous than *olivascens.* Hellmayr (1934) noted that two of nine specimens from Ecuador had a faint greyish tinge in the postocular region; he interpreted this as revealing the close relationship between *olivascens* and *peruana.* It is not clear, however, whether Hellmayr realized that juveniles of *olivascens* typically have a grey postocular area. Hellmayr (1934) included the preceding taxa as subspecies within *Cinnycerthia peruana* but considered the most southern subspecies, *fulva,* to be a separate species (*C. fulva*) based on its distinctly smaller size and well-defined buffy-white superciliary. Until Hellmayr's (1934) revision, *fulva* was not considered to be congeneric with the other taxa (all in *Cinnycerthia*), but was placed in the genus *Thryophilus.* Paynter (1960) placed *fulva* as a subspecies within *C. peruana* and retained the other three subspecies; no reasons were published for the merger of *fulva* into *peruana.* Subsequent works on South American birds have followed Paynter's treatment (e.g., Meyer de Schauensee 1966, 1970; Ridgely and Tudor 1989; Fjeldså and Krabbe 1990).

METHODS

We examined six mensural characters with dial calipers (measured to the nearest 0.05 mm) on 235 (118 males and 117 females, according to gonad information on label) study skins: (1) wing-length (chord of unflattened wing from bend of wing to longest primary); (2) bill-length (of exposed culmen); (3) bill-width (at its base); (4) bill-depth (at its base); (5) tail-length (measured from point of insertion of central rectrices to tip of longest rectrix); and (6) tarsus length (from the joint of tarsometatarsus and tibiotarsus to the lateral edge of last undivided scute). In addition to the specimens at the Museum of Natural Science, Louisiana State University (hereafter LSUMZ), specimens were examined from five other museums with major collections of Andean birds (see Acknowledgments).

Specimens in juvenal or downy plumage or with damaged, extensively worn or molting wing and tail feathers were excluded. Because many specimens in "adult" plumage lacked data on age (e.g., skull pneumatization), we also performed separate analyses using only those specimens with skull pneumatization ≥90% to determine the effect of inclusion of young birds

←

FIG. 1. Distribution of *Cinnycerthia* taxa based on samples included in this study. Triangles are *bogotensis,* dark circles are *olivascens,* hollow circles are *peruana,* and squares are *fulva.*

in adult plumage. Similarly, most specimens did not possess data on body mass, a potentially useful size character. Using only specimens of known mass, an ANOVA was used to detect sex and subspecies differences. Mass was not used in the multivariate analyses.

Geographic coordinates for each locality were taken from Paynter et al. (1975), Paynter and Traylor (1977, 1981), and Stephens and Traylor (1983). SAS software (SAS Institute, Inc. 1982) was used to calculate all univariate statistics and perform regressions, analyses of variance (ANOVA, MANOVA), principal component analyses (PCA), and discriminant function analyses (DFA). Morphometric data were $\log_{10}$-transformed for all analyses to correct for a non-normal distribution. All ANOVAs were two-way a posteriori comparisons of least squares means with the rejection level set according to the number of comparisons by using the Bonferroni method.

Plumage colors of the 235 specimens were compared to a published color standard (Ridgway 1912) under a combination of fluorescent and natural overhead lighting. For *bogotensis, olivascens* and *peruana,* the postocular area of each specimen was scored as (0) no postocular stripe evident, (1) postocular stripe inconspicuous, poorly demarcated, and probably not visible in the field, or (2) postocular stripe conspicuous, reasonably well-defined, and probably visible in the field. For all specimens, the amount of white feathering on the head (in *fulva* group, excluding the superciliary) was scored as (0) none, (1) partial or complete, small, white eye-ring, (2) a portion of the forecrown with white feathers, (3) both 1 and 2, (4) extensive white feathering on face and forecrown, or (5) much of the head white, especially most of the face and crown. Because the degree of development of the superciliary and the extent of white feathering on the head are continuously distributed characters, our scoring system reflects an arbitrary typology.

Specimens collected from the same region more than 70 years apart showed no sign of post-mortem color change. There is some seasonal variation in coloration caused by wear. For example, in nominate *peruana,* and especially in the *fulva* group, specimens from October to June tended to be more richly colored and ochraceous than those taken from July to September. This is the only Andean forest bird with which we are familiar that shows such seasonal plumage wear.

RESULTS

Sexual dimorphism.—ANOVAs of the six skin measurements indicate a significant ($P < 0.05$) sex effect on wing-length in all subspecies except *bogotensis* (Table 1). This was also found in the analysis of specimens with skull pneumatization ≥90%. Differentiation in other characters depend on the subspecies examined. The larger sample sizes of *olivascens* and *peruana* may account for their having significant sexual dimorphism in more characters than *fulva* or *bogotensis.* Because of the apparent differences between sexes, all subsequent analyses were performed separately on males and females.

Univariate geographic variation.—Except for wing length, bill length, and mass, males and females show similar patterns of mensural character differentiation among subspecies. ANOVAs indicate that wing, tail, and tarsus lengths are significantly different among all subspecies except between *bogotensis* and *olivascens.* Other differences depend on the subspecies compared (Table 1). The elimination of specimens lacking data on skull pneumatization caused a loss of significance in those compari-

TABLE 1

MORPHOMETRIC CHARACTER MEANS WITH STANDARD DEVIATIONS[a]

Character	Males			
	C. o. bogotensis	*C. o. olivascens*	*C. peruana*	*C. fulva*
Mass	—	25.9 ± 4.1 (15)#	*20.6 ± 1.7 (36)#	18.4 ± 2.7 (6)
Wing length	67.9 ± 0.6 (4)	69.5 ± 3.0 (42)#	*62.0 ± 1.6 (57)#	*57.9 ± 1.9 (14)#
Bill length	14.4 ± 0.7 (4)	14.1 ± 0.7 (42)	*13.3 ± 0.6 (56)#	*12.8 ± 0.8 (14)
Bill width	4.9 ± 0.1 (4)	5.2 ± 0.3 (43)	*4.8 ± 0.3 (56)	4.8 ± 0.2 (14)
Bill depth	5.1 ± 0.1 (4)	5.1 ± 0.2 (40)#	*4.7 ± 0.3 (56)	4.5 ± 0.2 (13)
Tail length	64.9 ± 1.2 (4)	65.4 ± 2.3 (41)#	*58.8 ± 1.9 (56)#	*54.9 ± 1.3 (14)
Tarsus length	25.3 ± 0.6 (4)	24.6 ± 1.3 (42)#	*23.1 ± 0.9 (55)#	*21.7 ± 1.1 (13)#
	Females			
Character	*C. o. bogotensis*	*C. o. olivascens*	*C. peruana*	*C. fulva*
Mass	—	23.0 ± 2.7 (22)#	*18.4 ± 1.3 (32)#	*14.8 ± 1.6 (10)
Wing length	68.3 ± 1.7 (5)	*65.9 ± 2.2 (52)#	*60.2 ± 2.2 (42)#	*55.3 ± 1.7 (18)#
Bill length	13.8 ± 0.1 (4)	14.0 ± 0.6 (51)	*12.8 ± 0.5 (42)#	12.6 ± 0.7 (17)
Bill width	5.1 ± 0.2 (5)	5.1 ± 0.3 (52)	*4.7 ± 0.2 (41)	4.7 ± 0.3 (18)
Bill depth	4.8 ± 0.5 (5)	4.9 ± 0.2 (49)#	*4.6 ± 0.2 (42)	4.5 ± 0.3 (16)
Tail length	62.5 ± 1.7 (5)	62.6 ± 2.5 (51)#	57.1 ± 2.1 (41)#	*53.3 ± 1.9 (18)
Tarsus length	24.4 ± 2.6 (5)	23.5 ± 1.3 (49)#	*22.4 ± 0.9 (42)#	*20.7 ± 0.8 (17)#

[a] Sample sizes are in parentheses.
* Significant difference between subspecies, $P < 0.05$.
# Significant difference between sexes, $P < 0.05$.

sons that were only weakly significant in the full analysis. Differences in wing length, tail length, and tarsus length remained strongly significant except in the comparison of *peruana* and *fulva*, for which tail length was no longer significantly different.

In all six size characters, *olivascens* differs significantly from its southern neighbor *peruana*. To determine whether the samples of *olivascens*

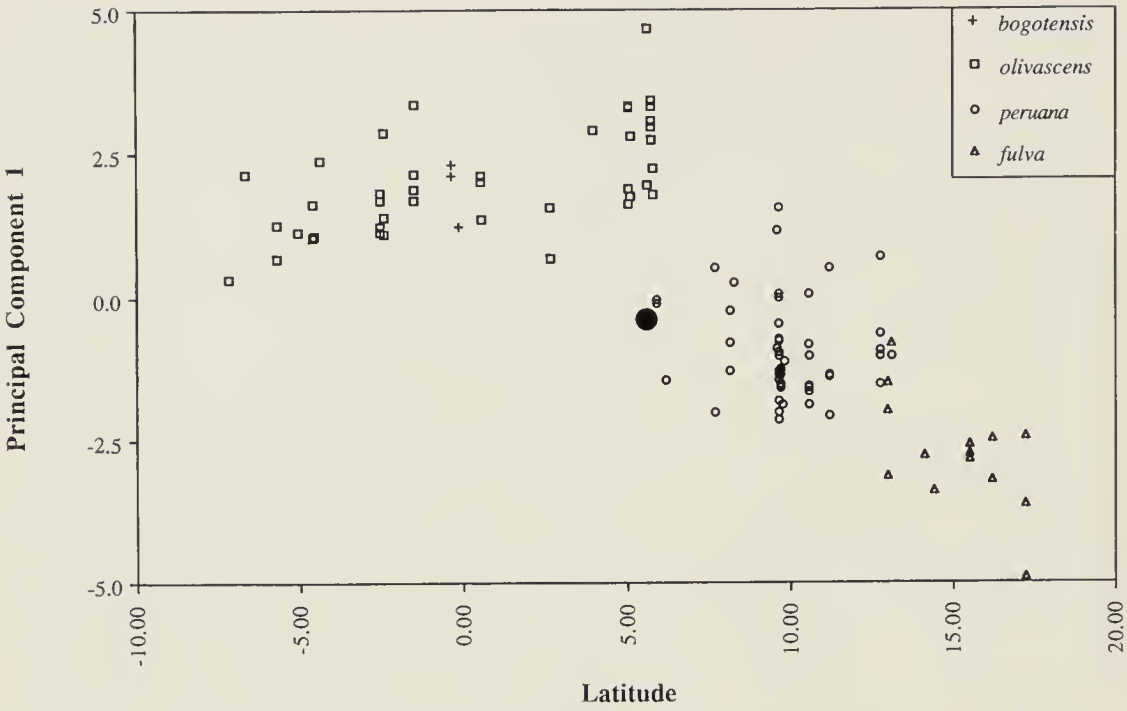

FIG. 2. Plot of first principal component axis against latitude in males. Larger circle denotes *olivascens* specimen that clusters with *peruana* (LSUMZ 88567). Negative numbers represent northern latitudes.

from north of the Equator contributed to a larger size difference between *olivascens* and *peruana* as a function of geographic distance, we used an ANOVA to compare populations of *olivascens* north and south of the equator. None of the morphometric characters showed significant differences in either sex.

A discrete size difference exists between *olivascens* and *peruana* where the two meet. Two adult *olivascens* (males: LSUMZ 117378, 11739) were taken on the east slope of the Cordillera Colán at "30 km by road E Florida on road to Rioja," depto. Amazonas. Only 16 km SW on the west slope of Colán four adult *peruana* from "33 road km NE Ingenio on road to Laguna Pomacochas," depto. Amazonas, were collected (males: LSUMZ 82126, 153098-9; female: LSUMZ 82125). A clue as to where the two taxa meet comes from a series taken east of La Peca Nueva. From site two, one male specimen (ca. 2680 m elev.; LSUMZ 88567; skull completely pneumatized) is *peruana* based on the morphometric characters (in multivariate space this individual sorts out with *peruana*; see large circle in Fig. 2). Although Graves (1980) considered this specimen as evidence for introgression because of a "few white feathers in the eye-ring," it is clearly typical of *peruana* in size and plumage as well as in presence of white feathers. The other nine specimens taken from the La

Peca Nueva sites are all *olivascens* based on size, and all lack white facial feathering. This suggests sympatry between the two forms without introgression. When individual skin measurements are compared for all west slope sites, the discrete difference in size between the two subspecies is apparent (Table 2).

In both sexes, *peruana* and *fulva* differ significantly in wing, tail, and tarsus lengths. Our most northern sample of *fulva* is from a northern spur of the Cordillera Vilcabamba (depto. Cuzco, Peru), a ridge bounded on the west by the "deeply incised" Apurímac Valley (Haffer 1974). Our southernmost sample of *peruana* is only 150 km NW on a slope of the Cordillera Occidental, west of the Apurímac (Yuraccyacu, depto. Ayacucho, Peru). All specimens except one of unknown age (female: American Museum of Natural History 820507; hereafter AMNH) are clear representatives of their respective subspecies (Table 2). The aberrant specimen was taken from the Cordillera Vilcabamba and is *peruana* in tail length.

Specimens from the Cordillera Vilcabamba represent a distinctive new subspecies based on plumage (Remsen and Brumfield, unpubl. data). Because these populations are allopatric from populations of *peruana* and *fulva* from the main Andes, they are less likely to show signs of introgression between the two forms. To determine if there is any evidence of introgression between *peruana* and *fulva,* we compared the southernmost samples of *peruana* (from Yuraccyacu) with our northern most sample of *fulva* from the main Andes (males: Field Museum of Natural History 311813–4, from Pillahuata, depto. Cuzco; hereafter FMNH). Although both *fulva* specimens were typical of *fulva* in wing-length, one individual (311814) was typical of *peruana* in both tail-length and tarsus-length, two characters that are reliable for distinguishing all subspecies except *bogotensis* (Table 2). This may indicate some introgression between populations of *fulva* from the main Andes and *peruana.*

North of the equator, the elevational distribution of specimens is not correlated with latitude (Spearman $r = 0.25$, ns). South of the equator, the elevations of specimens increase slightly but significantly with distance from the equator (Spearman $r = 0.29$, $P < 0.0005$). A MANOVA revealed that there is no significant elevation effect on the morphometric characters in either sex (Wilk's Lambda = 0.07, ns).

Multivariate geographic variation.—Because individual characters do not vary independently, we performed a principal component analysis to determine which variables best account for the variation expressed across the range of the species. In specimens missing one or two characters (N = 17), the subspecies mean was substituted for the missing value. Eigenvalues and eigenvectors were extracted from the correlation matrix. Load-

TABLE 2

INDIVIDUAL MEASUREMENTS OF SPECIMENS NEAR POTENTIAL CONTACT ZONES (REFER TO FIGURES 1 AND 2; SUBSPECIES MEANS ARE FOR ALL OTHER SPECIMENS)

	Mass	Wing length	Bill length	Bill width	Bill depth	Tail length	Tarsus length
				Males			
C. o. olivascens mean	25.9 ± 4.1	69.5 ± 3.0	14.1 ± 0.7	5.2 ± 0.3	5.1 ± 0.2	65.4 ± 2.3	24.6 ± 1.3
Fig. 2, site 2	20.5	63.7	13.3	5.0	4.7	60.8	23.3
Fig. 2, site 3	29.0	76.6	16.2	5.6	5.2	71.2	25.0
Fig. 2, site 3	25.0	67.5	15.7	5.2	5.0	62.8	23.7
Fig. 2, site 4	18.0	63.7	13.5	5.2	4.7	60.0	23.8
Fig. 2, site 4	17.0	61.7	14.7	5.4	4.9	58.6	21.3
C. peruana mean	20.6 ± 1.7	62.0 ± 1.6	13.3 ± 0.6	4.8 ± 0.3	4.7 ± 0.2	58.8 ± 1.9	23.1 ± 0.9
Yuraccyacu	—	61.0	13.5	5.2	4.6	59.7	23.2
Yuraccyacu	—	66.7	14.1	5.0	4.8	61.5	24.0
Yuraccyacu	—	59.0	13.5	4.8	4.9	58.9	22.7
Yuraccyacu	—	62.9	13.0	4.6	4.8	60.7	23.0
Yuraccyacu	—	60.9	13.2	4.6	4.8	57.9	22.3
Yuraccyacu	20.5	62.8	12.7	4.8	5.0	59.0	22.5
Pillahuata	19.2	58.6	13.4	5.2	4.7	57.0	24.4
Pillahuata	—	62.0	13.2	4.9	4.8	54.2	21.1
Cordillera Vilcabamba	—	59.5	12.3	4.9	4.3	55.8	21.2
Cordillera Vilcabamba	—	62.0	13.2	4.8	4.6	55.1	21.8
C. fulva mean	18.4 ± 2.7	57.9 ± 1.9	12.8 ± 0.8	4.8 ± 0.2	4.5 ± 0.2	54.9 ± 1.3	21.7 ± 1.1

TABLE 2
CONTINUED

	Mass	Wing length	Bill length	Bill width	Bill depth	Tail length	Tarsus length
				Females			
C. o. olivascens mean	23.0 ± 2.7	65.9 ± 2.2	14.0 ± 0.6	5.1 ± 0.3	4.9 ± 0.3	62.6 ± 2.5	23.5 ± 1.3
Fig. 2, site 1	25.0	67.7	14.2	5.3	5.1	66.0	24.2
Fig. 2, site 1	25.5	67.9	15.4	5.6	5.4	67.4	24.4
Fig. 2, site 1	25.5	67.7	15.3	5.4	4.8	66.8	24.0
Fig. 2, site 2	25.5	68.7	14.1	5.2	5.3	65.3	24.7
Fig. 2, site 3	24.0	69.0	14.5	5.3	4.9	64.2	24.8
Fig. 2, site 3	25.0	70.0	14.4	5.2	5.3	65.4	24.2
Fig. 2, site 3	27.0	66.5	14.6	5.5	5.0	65.3	24.9
Fig. 2, site 4	15.0	59.1	13.6	4.8	4.5	56.8	21.5
C. peruana mean	18.4 ± 1.3	60.2 ± 2.2	12.8 ± 0.5	4.7 ± 0.3	4.6 ± 0.2	57.1 ± 2.1	22.4 ± 0.9
Yuraccyacu	17.9	59.9	12.7	4.9	4.5	56.7	23.8
Cordillera Vilcabamba	—	52.8	12.4	4.5	4.5	54.4	20.8
Cordillera Vilcabamba	—	56.9	12.8	5.6	4.7	51.9	21.0
Cordillera Vilcabamba	—	55.8	12.8	5.2	4.9	53.1	19.7
Cordillera Vilcabamba	—	57.2	13.1	4.7	4.5	56.9	21.4
C. fulva mean	14.8 ± 1.6	55.3 ± 1.7	12.6 ± 0.7	4.7 ± 0.3	4.5 ± 0.3	53.3 ± 1.9	20.7 ± 0.8

TABLE 3
CHARACTER LOADINGS FROM PRINCIPAL COMPONENT ANALYSIS OF MORPHOMETRIC CHARACTERS

	PCA I		PCA II		PCA III	
	Males	Females	Males	Females	Males	Females
Wing length	0.458	0.451	−0.279	−0.294	−0.133	−0.173
Bill length	0.394	0.398	0.213	−0.341	−0.781	0.628
Bill width	0.322	0.361	0.854	0.630	0.327	0.293
Bill depth	0.408	0.372	−0.040	0.544	0.272	−0.056
Tail length	0.458	0.456	−0.183	−0.321	−0.038	0.051
Tarsus length	0.393	0.402	−0.335	−0.037	0.435	−0.695
Percentage of variance	62.7	63.8	12.2	11.7	8.3	8.8

ings on the first principal component (PCA 1) are large and positive (wing-length and tail-length had the highest loadings) for all characters (this was also found in an analysis of known adults) indicating that general size accounts for most (males 63%, females 64%) of the variation (Table 3).

A regression of PCA 1 against latitude illustrates a significant negative correlation between size and latitude in males both north ($r = -0.47$, $P < 0.05$, N = 26) and south ($r = -0.79$, $P < 0.0001$, N = 91) of the equator, and in females both north ($r = -0.47$ $P < 0.05$, N = 32) and south ($r = -0.79$, $P < 0.0001$, N = 85) of the equator (Fig. 2; Table 1). It should be noted that the two taxa that occur north of the equator, *bogotensis* and *olivascens,* were represented by small sample sizes from all collecting localities (Fig. 1). Latitudinal variation within populations south of the equator is interesting in that measurements of *olivascens* are positively correlated with latitude in both males ($r = 0.50$, $P < 0.05$, N = 21) and females ($r = 0.50$, $P < 0.05$, N = 24). Populations of *peruana,* with the greatest range in latitudinal sampling, however, show no significant correlation with latitude in either males ($r = 0.26$, ns, N = 56) or females ($r = 0.05$, ns, N = 42). Finally, populations of *fulva* are significantly negatively correlated with latitude in both males ($r = -0.62$, $P < 0.05$, N = 15) and females ($r = -0.51$, $P < 0.05$, N = 18). If the subspecies examined were the result of clinal variation (i.e., not distinct evolutionary units), then we would expect size to be negatively correlated with latitude both within as well as among subspecies. The subspecies with the best latitudinal sampling, *peruana,* showed no correlation of size with latitude. More samples of *bogotensis, olivascens,* and *fulva* are need-

ed to allow sufficient examination of clinal variation within each subspecies.

A discriminant function analysis was used to determine the percentage of specimens that could be classified correctly solely on size measurements. This analysis is similar to PCA, but assumes *a priori* the identification of the groups based on the museum label. By making this assumption, DFA can determine which characters cause maximal separation of the groups. We plotted discriminant functions for each specimen along an axis. Specimens were considered unidentifiable if their discriminant function value overlapped with any values from their neighbor taxon. Specimens of *bogotensis* could not be distinguished from *olivascens*. When compared only to each other, 79% of *olivascens* and 92% of *peruana* were identified unambiguously. When compared only to each other, 87% of *peruana* and 73% of *fulva* were identified unambiguously. All unidentifiable specimens were examined individually for geographic proximity to their neighbor taxon and size relative to the rest of their taxon. Most unidentifiable specimens occurred far from their neighbor taxon and, therefore, probably represent extreme within-subspecies variation and not introgression from subspecific neighbors. Three of the five individuals from our most northern specimens of *fulva* (Cordillera Vilcabamba), however, could not be differentiated from *peruana* based on size measurements. These three are, however, unambiguously diagnosable based on plumage (presence of buffy-white superciliary stripe in *fulva*).

Plumage Coloration

1. Eastern Andes of Colombia and bogotensis.—Beginning near the northeastern extreme of latitudinal distribution of our sample, specimens examined (N = 14) from the eastern Andes of Colombia (deptos. Huila, Putumayo, and Nariño) can be distinguished from other populations in the Andes of Colombia and Ecuador by their darker, redder brown underparts. In being darker than *olivascens,* these specimens match Hellmayr's (1934) brief notes on *bogotensis,* which were described from "Bogotá" specimens that lacked precise locality data. However, we were unable to locate specimens from the possibly disjunct population (see map in Hilty and Brown 1986) farther north in deptos. Santander, Boyacá, and Cundinamarca, a region more likely to contain the true type locality for "Bogotá" specimens, as noted for this taxon in particular by Olivares (1969). Hellmayr (1934), who examined the type specimen of *bogotensis,* assigned a specimen from Andalucia, depto. Huila (presumably the same specimen in our sample, AMNH 116874) to this taxon. Therefore, we treated our sample as *bogotensis* but with some hesitancy. In any case, these specimens differ strongly from our nearest specimens from adjacent

Ecuador in depto. Napo in being a darker, richer, redder (particularly in depto. Nariño) brown on the underparts, closer to Prout's Brown or Van Dyke Brown than to the Cinnamon Brown or Saccardo's Umber of the Ecuadorian specimens, and in having much darker throats. Such levels of differentiation in color are typically accorded subspecies status.

2. *Central and western Andes of Colombia to northern Peru.*—Populations from the central Andes and the western Andes of Colombia, the eastern Andes of Ecuador, the eastern Andes of Peru north of the Marañón Valley, and some localities south of the Marañon in the eastern Andes of extreme northern depto. Amazonas, Peru, are all similar in general coloration. Their underparts are fairly dark brown, closest to Cinnamon Brown or Saccardo's Umber, with the throats slightly paler; their upperparts are an even darker brown, closest to Chestnut Brown or Van Dyke Brown, with a paler, often ochraceous-tinged forecrown. We are unable to distinguish by using any color character the specimens from the two extremes in latitudinal distribution (central Colombia vs. northern Peru), except that populations from Ecuador south to Peru show an increasing tendency towards having a trace of a postocular stripe (Table 4). Also, several specimens from Colombia have white feathering on the forehead, a feature not yet known from populations from Ecuador and Peru. These populations represent the taxon *olivascens,* the type locality of which is Santa Elena on the eastern slope of the Central Andes near the northern limit of the taxon. We found only one specimen each from the western Andes of Colombia and Ecuador. Both are within the range of color of *olivascens.*

In northern Peru, where *olivascens* meets nominate *peruana,* geographic variation in color is complex. All but one specimen from three localities in extreme northern Peru on both sides of the Marañón River are virtually indistinguishable from one another. These specimens are from (1) the Cerro Chinguela area in depto. Cajamarca, north of the Marañón (see Parker et al. 1985), (2) the Cordillera Colán area in central depto. Amazonas, south of the Marañón, and (3) the Abra Patricia area in extreme northern depto. San Martín. The only difference between the populations on opposite sides of the Marañón was a tendency towards faint postocular stripes in populations on the south side (Table 4). These represent the southernmost populations of what is currently considered *C. p. olivascens* (Fjeldså and Krabbe 1990).

However, one specimen from Cordillera Colán (ca 2680 m elev.; LSUMZ 88567; skull completely pneumatized) differs dramatically from the other 11 from the region in being paler and less reddish throughout and in having a distinct postocular streak. As noted above, it is also distinctly smaller than males from the same area (wing-length 63.7 mm

TABLE 4

PROMINENCE OF POSTOCULAR AREA IN POPULATIONS OF *CINNYCERTHIA* Wrens in Peru
(Numbers in Rows Refer to the Number of Specimens with Each Score)

Taxon Region[a]	Postocular score		
	0[b]	1[c]	2[d]
C. o. bogotensis			
E. Andes	7	0	0
C. o. new subspecies?			
depto. Nariño	8	0	0
C. o. olivascens			
W. Andes (e. slope), Colombia	19	0	0
Central Andes, Colombia	7	0	0
Ecuador	14	2	0
depto. Cajamarca	15	0	0
Cordillera Colán	9	2	0
Abra Patricia	2	4	0
Total (*C. o. olivascens*)	66 (89%)	8 (11%)	0
C. peruana			
Cordillera Colán	0	0	1
Ne. of Ingenio; La Lejia	0	0	4
Puerta del Monte	0	0	4
depto. La Libertad	0	6	6
depto. Huánuco	1	31	2
depto. Pasco	2	23	2
depto. Junín	0	14	4
depto. Ayacucho	0	7	0
Total (*C. peruana*)	3 (3%)	81 (76%)	23 (21%)

[a] Arranged from north to south.
[b] 0 = No postocular stripe evident.
[c] 1 = Postocular stripe inconspicuous, poorly demarcated, and probably not visible in the field.
[d] 2 = Postocular stripe conspicuous, reasonably well-defined, and probably visible in the field.

vs. 72.0 mm average for other two males), and it also has an indistinct white eye-ring, a condition found in many specimens of nominate *peruana* but unknown in *olivascens*. In these respects, therefore, it matches specimens of nominate *peruana* from localities to the south. It differs, however, from nominate *peruana* from deptos. San Martín and La Libertad in being less ochraceous. As noted above, Graves (1980) considered this specimen to be an *olivascens* with signs of introgression from nominate *peruana*. However, other than being collected in the same area as true *olivascens*, it has no characters of that taxon, and its paler, less reddish coloration is not really intermediate between that of *olivascens* and

typically more ochraceous *peruana*. For those reasons, Graves (pers. comm.), with a much larger series of specimens available to him than in 1980, now considers the specimen to represent *peruana* and not an intergrade. Because *Cinnycerthia* wrens are sedentary, secretive, undergrowth-dwelling species with short, rounded wings, it seems unlikely that this individual represented a long-distance wanderer, but rather a sympatric resident population.

Three adults from "33 road km NE Ingenio on road to Laguna Pomacochas," depto. Amazonas (LSUMZ 82125-26, 153098; elevs. ca. 2315 and 2135 m), are like typical nominate *peruana* in having prominent postocular streaks (Table 4), in being a paler, less reddish brown overall, and in being small (see Morphometrics section above). One (female: LSUMZ 82125) is distinctly ochraceous on the underparts and has a white eye-ring and whitish feathers on the forehead; it is indistinguishable from nominate *peruana*. The other two (both males), however, lack the ochraceous tones and are virtually identical to LSUMZ 88567 from Cordillera Colán; one has a partial white eye-ring. The locality from which these three specimens come is just south of the main part of the Cordillera Colán and only about 10 km from localities that have typical *olivascens*. This locality, however, is also between the Cordillera Colán and a locality farther southeast, Abra Patricia, where typical *olivascens* is found. Another specimen (male: AMNH 234998) from slightly farther south at La Lejia, N. of Chachapoyas, depto. Amazonas, is slightly less reddish throughout and less ochraceous on the throat than typical nominate *peruana* from farther south, but it is more reddish throughout than the three above-mentioned specimens. We suspect that a thorough elevational transect in this region would show that, where the two taxa come together, *olivascens* will be found at high elevations and *peruana* at low elevations.

Whether the above specimens represent intermediates between *olivascens* and nominate *peruana* or whether they represent geographic variation at the northern extreme of nominate *peruana* cannot be determined without larger series of specimens, preferably accompanied by genetic samples. We currently favor the latter treatment because the specimens in question are like nominate *peruana* in size, presence of white facial feathering, and prominence of the postocular streak. The only tendency towards nominate *peruana* in the series of *olivascens* in the region is the presence of class 1 postocular streaks in some specimens (Table 4). Therefore, if there is gene flow between the populations, it is only faintly expressed in the phenotypes of the populations there. The differences between nominate *peruana* and *olivascens* are of the same general magnitude as those between *olivascens* and *C. unirufa*, which are clearly two separate species (Hellmayr 1934, Parker et al. 1985). We therefore believe

that the burden of proof falls on those who would treat *olivascens* and nominate *peruana* as a single, freely interbreeding biological species, and we regard *C. olivascens* Sharpe as a separate species. We propose "Sharpe's Wren" as an English name for *C. olivascens* and "Peruvian Wren," the name used by Hellmayr (1934), for *C. peruana,* which is endemic to Peru.

3. Eastern Andes of central Peru.—A series of 106 adult specimens from Puerta del Monte, depto. San Martín, south through deptos. La Libertad, Huánuco, Pasco, Junín, and Ayacucho are all relatively uniform in coloration but with some individual variation that shows little geographic pattern. Their upperparts are a dark, rich brown closest to Brussels Brown or Russet Brown but darker; most specimens have an ochraceous tinge to the forecrown. Their underparts are generally closest to Cinnamon Brown. Their throats range from buffy white to ochraceous. All but three specimens have either a class 1 or class 2 postocular streak (Table 4), and 38% (N = 41) have some white feathering on the head (Table 5). We concur with Graves (1980) that this white feathering is found only on birds with nearly or completely pneumatized skulls and that it is found in both males and females (cf. Gochfeld 1979).

4. Eastern Andes of southern Peru and northern Bolivia.—Reference works (Paynter 1960, Ridgely and Tudor 1989, Fjeldså and Krabbe 1990) currently treat all populations from depto. Cuzco, Peru, south to depto. Cochabamba, Bolivia, as one taxon, *C. peruana fulva.* However, this region includes at least three discrete taxa, as we outline below.

At the northern extreme in latitude of this region, specimens (N = 7) from the isolated Cordillera Vilcabamba, depto. Cuzco, differ dramatically from any other *Cinnycerthia* wren in having a well-defined dark crown. These are clearly a distinct, undescribed taxon most closely related to *C.* {*p*}. *fulva* (Remsen and Brumfield, unpubl. data). The Cordillera Vilcabamba specimens do not, however, differ significantly in any size character from *fulva* populations in Cuzco or depto. Puno, Peru, south to depto. Cochabamba, Bolivia.

The type locality of *fulva* is in the main Andes of depto. Cuzco. Unfortunately, few specimens of *fulva* have been collected in that region, and these wrens are notably rare there (T. A. Parker, pers. comm.); in fact, we can find no specimens or published localities from west of the Río Apurímac Valley through the Urubamba drainage east to at least the Río Paucartambo valley. Because humid forest in this region has been thoroughly sampled (e.g., Chapman 1921, Parker and O'Neill 1980), we suspect that the absence of *Cinnycerthia* wrens in this region may be a true gap in their distribution. In addition to the type specimen, taken at Huasampilla, we found only two other specimens in depto. Cuzco; all three are in the Río Madre de Dios drainage in the humid eastern portion

TABLE 5

AMOUNT OF WHITE FEATHERING ON HEAD IN POPULATIONS OF *CINNYCERTHIA* WRENS IN PERU AND BOLIVIA (NUMBERS IN ROWS REFER TO THE NUMBER OF SPECIMENS WITH EACH SCORE)

Taxon Region	White head-feathering score[a]					
	0	1	2	3	4	5
C. o. bogotensis						
E. Andes	5	0	2	0	0	0
C. o. new subspecies?						
depto. Nariño	5	0	2	0	1	0
C. o. olivascens						
W. Andes (e. slope), Colombia	13	0	5	1	0	0
Central Andes, Colombia	5	0	2	0	0	0
Ecuador	16	0	0	0	0	0
depto. Cajamarca	15	0	0	0	0	0
Cordillera Colán	11	0	0	0	0	0
Abra Patricia	5	0	0	0	0	0
Total (*C. o. olivascens*)	65 (89%)	0	7 (10%)	1 (1%)	0	0
C. peruana						
Cordillera Colán	0	1	0	0	0	0
Ne. of Ingenio; La Lejia	2	1	0	1	0	0
Puerta del Monte	2	0	0	0	1	0
depto. La Libertad	8	2	0	1	1	0
depto. Huánuco	19	3	1	2	8	3
depto. Pasco	20	2	0	1	4	0
depto. Junín	13	1	0	2	2	0
depto. Ayacucho	3	0	1	2	1	0
Total (*C. peruana*)	67 (62%)	10 (9%)	2 (2%)	9 (8%)	17 (16%)	3 (3%)

TABLE 5
CONTINUED

Taxon / Region	White head-feathering score[a]					
	0	1	2	3	4	5
C. fulva group						
Vilcabamba (subsp. nov.)	6	0	1	0	0	0
depto. Cuzco	2	0	0	0	0	0
depto. Puno	4	0	3	1	0	0
depto. La Paz	10	0	4	2	0	0
depto. Cochabamba	6	0	0	0	0	0
Total (*C. fulva* group)	28 (72%)	0	8 (21%)	3 (8%)	0	0

[a] The amount of white feathering on the head (in *fulva*, excluding the superciliary) was scored as: (0) none; (1) partial or complete, small, white eye-ring; (2) a portion of the forecrown with white feathers; (3) both 1 and 2; (4) extensive white feathering on face and forecrown; or (5) much of the head white, especially most of the face and crown.

of the departamento. The two specimens that we examined (FMNH 311813–814, from Pillahuata) are extremely similar to each other and differ dramatically from specimens from depto. Puno, Peru, to depto. Cochabamba, Bolivia, in having a superciliary that is less conspicuous because it is ochraceous rather than buff-white, and because it is not as broad. Also, the broad, dark eye-line is less conspicuous because the auriculars are much darker, and the back and underparts are slightly darker. In these features, the Cuzco specimens could be regarded as showing variation in the direction of *peruana.* We suspect that this is why Paynter (1960) merged *fulva* into *peruana.* Even if the gap in distribution in western depto. Cuzco is a sampling artifact, *peruana* would be separated from *fulva* by the canyon of the Río Urubamba, and so no test of sympatry is possible for direct assessment of species limits. Therefore, whether *peruana* and *fulva* should be treated as different biological species depends on the importance one assigns to the apparent variation towards *peruana* shown in Cuzco specimens of *fulva.*

We propose that *fulva* be elevated to species status because *fulva,* particularly those populations from the Cordillera Vilcabamba and those from depto. Puno south, differs in plumage pattern more than *peruana* does from *C. olivascens* or than even *C. olivascens* does from *C. unirufa.* All populations currently included in *fulva* differ from *C. peruana* in having a distinctive, well-defined superciliary that extends from the forecrown at the nares posteriorly to the nape. The auriculars are pale like the superciliary, thereby sharply demarcating a broad, dark eye-stripe, and the auriculars are only slightly darker than the pale throat. Thus, *fulva* has a patterned face, with a conspicuous pale superciliary and dark eye-stripe, whereas *peruana,* which only occasionally has a hint of a postocular superciliary on an otherwise uniform reddish-brown face, has no face pattern. The head pattern of *fulva* gives the bird a different "look" from *C. peruana,* a difference that doubtless led to these populations' original placement in a different genus, *Thryophilus* (now merged in *Thryothorus*). As noted by Ridgely and Tudor (1989), the face pattern of *fulva* recalls that of the sympatric Mountain Wren (*Troglodytes solstitialis*). The rest of the plumage, however, is similar to other *Cinnycerthia* species. The breast and belly, closest to a pale dull Sayal Brown, are paler and less reddish than those of *C. peruana.* The upperparts are like those of *C. peruana* but are also paler and slightly less reddish. Finally, the extensive white feathering found in some *peruana* is unknown in *fulva* (Table 5). We propose that Hellmayr's (1934) English name for *fulva,* "Superciliated Wren," be used for this species. We suspect that comparisons of vocalizations will be especially important in resolving species

limits; T. A. Parker (pers. comm.) has observed that *fulva* is rather quiet compared to the often noisy *peruana*.

The distinctively small, pale specimens from depto. Puno, Peru, and deptos. La Paz and Cochabamba, Bolivia, seem to be indistinguishable from one another in plumage or size; the paleness of a recent LSUMZ series of 13 July-August specimens from the Chuspipata region of La Paz seems attributable to seasonal wear. The Puno-to-Cochabamba population represents an undescribed subspecies (Remsen and Brumfield, unpubl. data) that differs from the depto. Cuzco population in the ways described above.

Although white facial feathering has been reported in *C. peruana sensu latu* from Ecuador south (Fjeldså and Krabbe 1990), we cannot find any explicit reference to such white feathering in *fulva*. In a series of 39 adults of *fulva* from depto. Puno to depto. Cochabamba, eight individuals show "extra" white feathers on the forecrown above the superciliary and three of these have "extra" white feathers around the eyes (Table 5); none, however, shows the class 4 or class 5 white feathering found regularly in *peruana*.

DISCUSSION

Zoogeography.—Somewhere in the Eastern Andes of extreme northern Ecuador or southern Colombia, *bogotensis* must meet *olivascens*. We know of no geographic barriers in the region that might separate the two. The southern limit of *olivascens* also does not correspond to any prominent geographic boundary. The deep, arid Marañón valley has long been recognized as a major barrier to dispersal for birds occurring in humid montane forest. Parker et al. (1985) noted 18 pairs of allospecies separated by the Río Marañón. However, *C. olivascens* is found on both sides of the barrier, and our limited samples suggest that it interdigitates with *C. peruana* in the Andes just south of the Marañón. The southern limit of *peruana* corresponds to one of the most important biogeographic boundaries in the humid Andes, the Río Apurímac valley (Haffer 1974).

The distinctive new subspecies of *fulva* in the Cordillera Vilcabamba adds another taxon endemic to this major outlying range. The gap in distribution between the distinctive taxon in the Cordillera Vilcabamba and the range of nominate *fulva* in southeastern depto. Cuzco is a pattern also found in the Rufous-naped Brush-Finch (*Atlapetes rufinucha*) (Remsen 1993).

Nominate *fulva* and the undescribed southern subspecies must meet somewhere in southern depto. Cuzco or northern depto. Puno. Several other pairs of Andean bird taxa share this pattern (e.g., Marcapata Spinetail [*Cranioleuca marcapatae*] and Light-crowned Spinetail [*C. albi-*

ceps], Remsen 1984b; White-throated Spadebill [*Platyrinchus mystaceus zamorae* and *P. m. partridgei*], Remsen et al. 1991). Precisely where this turnover takes place is not known, but the most likely geographic barrier in the region is the Río Marcapata valley in extreme southeastern depto. Cuzco.

Species limits.—Our analysis of geographic variation in plumage and morphology in populations currently treated as *Cinnycerthia peruana* supports recognition of three biological species. The northernmost, *olivascens,* shows large, discrete morphometric differences from the next population to the south, *peruana,* as well as marked plumage differences. Some specimens in the region of contact, however, have intermediate plumage characters that could be interpreted as evidence of past or present gene flow. The presence of these two different forms in such geographic proximity suggests that either an abrupt step cline serves to differentiate the groups or, more likely, past geological events (e.g., Río Marañón) isolated the forms long enough for differentiation to occur. The absence of unambiguously intermediate forms and the presence of an individual of *peruana* within a population of *olivascens* suggest that these two taxa are best treated as separate but closely related species.

Although contact between *peruana* and *fulva* is prevented by the Apurímac Valley, the distinctive plumage pattern of *fulva* relative to other *Cinnycerthia* species suggests that *fulva* should be treated as a separate species; in fact, no reason was ever published for the merger (by Paynter 1960) of *fulva* into *peruana.*

In summary, we recommend the following taxonomic treatment:

Cinnycerthia olivascens Sharpe's Wren
- *C. o. bogotensis* (eastern Andes of Colombia)
- *C. o. olivascens* (central Andes and western Andes of Colombia, eastern Andes of Ecuador, eastern Andes of Peru south extreme northern depto. Amazonas, Peru)

Cinnycerthia peruana Peruvian Wren (eastern Andes of Peru from depto. Amazonas to depto. Ayacucho)

Cinnycerthia fulva Superciliated Wren
- *C. f.* (undescribed subspecies) (Cordillera Vilcabamba, depto. Cuzco, Peru)
- *C. f. fulva* (eastern Andes of depto. Cuzco, Peru)
- *C. f.* (undescribed subspecies) (depto. Puno, Peru, to depto. Cochabamba, Bolivia)

Bergmann's Rule.—The linearity of the distributions of Andean forest birds (Remsen 1984a, Graves 1988) creates a unique opportunity to assess

Bergmann's Rule, which predicts that the body size of organisms increases in colder and drier areas as a response to changes in climatic conditions (James 1970). Although climatological data are unavailable for the humid Andes, we assume that temperatures in the Andes are colder with increasing distance from the Equator; rainfall data from LSUMZ collecting localities in Peru and Bolivia also suggest that localities farthest from the equator are drier. The elevational distribution of our specimen localities remains constant over latitude north of the Equator and increases with latitude south of the equator. Therefore, we do not believe that elevation per se is a variable that would influence body size, or if so, the influence would be in producing colder temperatures with increasing elevations south of the Equator.

Although Bergmann's Rule, including both the pattern and the explanation for the pattern (James 1970), seems deeply entrenched in vertebrate biology, 68% of the studies on intraspecific variation compiled by Peters (1992) do not support the rule (see also McNab 1971, Zink and Remsen 1986, Geist 1987). Only four studies have investigated Bergmann's rule in Andean birds. Graves (1991) found a positive correlation between body size and latitude in the Carbonated Flowerpiercer (*Diglossa carbonaria*) in both directions away from the equator, as did Kratter (1993) for the Yellow-billed Cacique (*Amblycercus holosericeus*). Remsen et al. (1991) found that body size in the White-throated Spadebill (*Platyrinchus mystaceus*) decreased south of the equator, counter to the prediction of Bergmann's rule, but the analysis included only populations south of the equator. Additionally, Remsen (1993) found that body size decreased away from the equator in *Atlapetes rufinucha,* but only those populations from depto. Cuzco (13°S. Lat.) to depto. Santa Cruz, Bolivia (18°S. Lat.) were analyzed. Although Bergmann's Rule is intended to apply primarily to intraspecific variation, we believe that its application to allopatric sister-species (allospecies), as in the *Cinnycerthia* populations analyzed herein, is also appropriate. Our results indicate that body size is negatively correlated with latitude in *Cinnycerthia* wrens both north and south of the equator, counter to Bergmann's Rule. The only exception appears within populations of *olivascens* south of the equator, where size may be positively correlated with latitude. Obviously, congruence between large numbers of a wide variety of taxa is necessary to determine the applicability of Bergmann's "Rule" to Andean birds.

ACKNOWLEDGMENTS

We thank the curatorial staffs of the Academy of Natural Sciences of Philadelphia, American Museum of Natural History (New York), Carnegie Museum of Natural History (Pittsburgh), Field Museum of Natural History (Chicago), and Delaware Museum of Natural

History (Dover) for generous loans of specimens. We thank A. P. Capparella, R. T. Chesser, J. C. Coulson, G. R. Graves, A. W. Kratter, T. S. Schulenberg, D. A. Wiedenfeld, and two anonymous reviewers for providing helpful comments on the manuscript. G. R. Graves re-examined material from northern Peru. J. M. Bates, S. J. Hackett, T. A. Parker III, K. V. Rosenberg, and T. S. Schulenberg provided to RTB immeasurable help and encouragement in the project's development. S. A. Juliano assisted with statistical analyses. The morphometric analyses of this paper initially were prepared by RTB as a research project for JVR's ornithology course.

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Wilson Bull., 108(2), 1996, pp. 228–245

NEST ATTENTIVENESS IN HUMMINGBIRDS

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Abstract.—With few exceptions, nest building, incubation, and care of young are the responsibilities of the female in hummingbirds (Trochilidae). The time females spent on these tasks (collectively defined as attentiveness) was determined for three species of hummingbirds nesting in southeastern Arizona and southwestern New Mexico, i.e., the Broad-billed (*Cynanthus latirostris*), Violet-crowned (*Amazilia violiceps*), and Black-chinned (*Archilochus alexandri*) hummingbirds. In addition to elucidating attentiveness, the data from my study also provide insights into the allocation of time for maintenance and other activities. This information, combined with that from other studies, shows a remarkable uniformity in attentiveness in the Trochilidae regardless of the taxa or geographic areas involved.
Received 1 Mar. 1994, accepted 15 Aug. 1995.

With few exceptions, nest building, incubation, and care of young are the responsibilities of the female in hummingbirds, with males rarely participating in reproduction beyond copulation. In addition to carrying out these responsibilities, female hummingbirds must also tend to their own needs, such as food procurement, plumage maintenance, and predator avoidance. The allocation of time to this array of tasks is also influenced by a number of other factors, including the availability of resources, weather conditions, and interactions among individuals and taxa. With such factors and the demands of non-reproductive activities in mind, I examined nest attentiveness in nesting Broad-billed (*Cynanthus latirostris*), Violet-crowned (*Amazilia violiceps*), and Black-chinned (*Archilochus alexandri*) hummingbirds in southwestern New Mexico and southeastern Arizona. My focus was on determining the time allotted by individual females to the tasks of nest building, incubation, and care of young. These findings are presented along with comparisons to hummingbird attentiveness in other studies. In general, hummingbirds show similar attentiveness patterns, particularly as regards incubation and to lesser degrees with other stages of the reproductive cycle.

STUDY AREAS AND METHODS

Three areas were selected for this study; all lacked artificial food sources such as hummingbird feeders or extensive areas of cultivated plants. The first and largest of these was Guadalupe Canyon, situated along the United States-Mexico border in southwestern New Mexico (Hidalgo Co.) and southeastern Arizona (Cochise Co.). Hummingbirds regularly nesting in this area include the Broad-billed, Violet-crowned, and Black-chinned, while Costa's Hummingbird (*Calypte costae*) nests occasionally (Baltosser 1986b, 1989a, 1989b) and the Lucifer Hummingbird (*Calothorax lucifer*) has nested at least once (Scott 1994).

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The second area was a segment of Rucker Canyon which lies on the west side of the Chiricahua Mountains in Cochise Co. in southeastern Arizona. Black-chinned Hummingbirds were the primary species at this site, with a few Magnificent Hummingbirds (*Eugenes fulgens*) also nesting (Baltosser 1986b). The third and most northern of the areas was along the Gila River near the town of Cliff, Grant County, New Mexico (Baltosser 1986a). The Black-chinned Hummingbird was the only hummingbird to nest at this site (for map and extensive description of each area see Baltosser 1986b).

I recorded periods of attentiveness in nesting female hummingbirds during 209 h of observation in the summer of 1976. My data sets are based on six nests and 17.5 h of observation for Broad-billed Hummingbirds, five nests and 26.1 h for Violet-crowned Hummingbirds, and 46 nests and 165.6 h for Black-chinned Hummingbirds (25 nests and 67.4 h for Guadalupe Canyon, 11 nests and 50.5 h for Rucker Canyon, and 10 nests and 47.7 h for Cliff). Only sessions (attentive periods) and recesses (periods away from nest) thought to have begun and ended spontaneously have been included in my study in order to eliminate unnaturally short or long intervals (see Skutch 1962). Nests were randomly selected for intensive study (stratified random sampling) and they were monitored from vantage points far enough away to prevent my interfering with natural events. Events were timed using a stopwatch and chronicled with the aid of a tape recorder.

My periods of observation were 1–4 h, and I stratified these into morning (06:00–10:00), mid-day (11:00–16:00), and evening (17:00–20:30) segments to gather data when ambient temperatures were lowest (morning hours), highest (mid-day), and intermediate (evening). Observations scheduled in this manner also allowed me to gather data for the period following the nocturnal fast (morning) and prior to the onset of fasting (evening). A tally of the hours that I devoted to each period by species and area was maintained, so that the observer effort would be similar for each.

Observations of nest attentiveness were further broken down by stage of the nesting cycle, which I categorized as (1) nest construction, (2) incubation, (3) care of smaller young, and (4) care of larger young. My reason for having two categories for the care of young was to allow for the detection of any differences in attentiveness due to differences that might exist in the energy needs of the chicks. Small young in my study are defined as nestlings of approximately 1–7 days in age, whereas large young are defined as nestlings in excess of seven days of age.

In this study, I depict nest attentiveness in terms of the average duration (data pooled) of sessions and recesses for each stage, species, and area. These data have in turn been standardized to compare the frequency of the females' arrivals and departures (number on/off bouts) on an hourly basis (collectively referred to as their activity budget). Diurnal fluctuations in attentiveness (e.g., morning vs evening) are based on the duration of sessions and recesses during morning, mid-day, and evening periods. Data within these three periods were averaged and then ranked for each species, stage of nesting, and area. Rankings show the relative duration of sessions and recesses throughout the day (e.g., morning sessions the shortest of the day, afternoon sessions the longest, and evening sessions of intermediate duration). The frequency of "unscheduled" disruptions (e.g., sudden presence of a conspecific, another species, predator, or a passing vehicle near the nest) and their influence upon attentive patterns was enumerated via direct observation.

Statistical comparisons were made using nonparametric analyses of variance (Kruskal-Wallis), coupled with multiple comparison tests (see Day and Quinn 1989). Modified nonparametric Student-Newman-Keuls' multiple range tests (SNK) and Tukey's honestly significant difference tests (HSD) were used because they represent the extremes in performance of *a posteriori* multiple comparison methods (Pimentel and Smith 1990). SNK tends to form too many nonsignificant subsets (high error rate) and HSD too few (lower error

TABLE 1

DURATION (MIN) OF SESSIONS (ON) AND RECESSES (OFF) OF HUMMINGBIRDS IN GUADALUPE CANYON FOR ALL STAGES OF NESTING[a]

	Broad-billed (A)		Violet-crowned (B)		Black-chinned (C)		Significance among species (*)		
Stage	On	Off	On	Off	On	Off	Species	On	Off
Construction	N = 1		N = 1		N = 8				
Mean	1.5	1.1	0.6	0.5	1.2	3.0	A-B	—	—
SD	2.1	0.7	0.2	0.04	0.7	2.7	A-C	—	—
Effort	6.1	3.2	42.2	29.6	194.6	480.8	B-C	*	*
Incubation	N = 3		N = 2		N = 16				
Mean	17.3	4.7	15.1	5.6	9.1	3.8	A-B		
SD	7.6	1.9	8.2	1.5	5.8	2.4	A-C	*	
Effort	435.0	125.4	247.9	101.3	1274.8	520.1	B-C		
Small young			N = 1		N = 4				
Mean	—	—	10.2	7.1	5.5	9.9	A-B	—	—
SD	—	—	4.4	0.5	2.8	6.8	A-C	—	—
Effort	—	—	165.5	126.2	314.0	405.1	B-C		
Large young	N = 2		N = 3		N = 5				
Mean	2.2	17.9	0.8	22.8	1.8	26.7	A-B		
SD	2.0	5.5	0.3	10.4	1.7	9.8	A-C		
Effort	49.9	209.7	24.7	658.2	45.2	475.2	B-C		

[a] N = Number of nests sampled, Effort = total observation time (minutes).

rate). I used SNK to gauge the results of HSD and, of 72 comparisons, the two methods differed in only 14 instances (19%). The 14 differences were distributed among the four stages as follows: construction (12%), incubation (4%), small-young (3%), and large-young (0%). I have been conservative in that my findings are based on Tukey's HSD, with the level of significance set at $P < 0.05$.

RESULTS

Duration of Alternating Bouts

Hummingbirds in Guadalupe Canyon.—During nest construction a rapid pace of sessions and recesses occurs (Table 1), punctuated by extended recesses. Black-chins completed an average of 10 on/off bouts averaging 1.2 and 3.0 minutes, respectively, before taking recesses that averaged 15.8 min. Violet-crowns completed an average of 14 on/off bouts before recesses averaging 9.2 min were taken. Data for Broad-bills are limited, but additional observations (untimed) suggest that attentiveness in nest construction is similar to the above. Attentiveness among species for the remaining stages of the nesting cycle showed generally similar patterns (Table 1). The only significant differences in incubation were in the length

TABLE 2

DURATION (MIN) OF SESSIONS (ON) AND RECESSES (OFF) OF BLACK-CHINNED HUMMINGBIRDS AMONG THREE AREAS FOR ALL STAGES OF NESTING[a]

Stage	Guadalupe (G)		Rucker (R)		Cliff (C)		Significance among areas (*)		
	On	Off	On	Off	On	Off	Area	On	Off
Construction	N = 8		N = 1		N = 2				
Mean	1.2	3.0	0.9	2.4	0.5	0.5	G-R		
SD	0.7	2.5	0.4	1.6	0.3	0.01	G-C	*	*
Effort[a]	194.6	480.8	11.4	21.5	16.4	24.5	R-C	*	
Incubation	N = 16		N = 10		N = 7				
Mean	9.1	3.8	8.9	3.9	17.1	7.0	G-R		
SD	5.8	2.4	4.9	2.2	10.4	3.0	G-C	*	*
Effort[a]	1274.8	520.1	863.8	339.0	545.9	224.9	R-C	*	*
Small young	N = 4		N = 3		N = 5				
Mean	5.5	9.9	13.1	17.0	11.7	12.8	G-R	*	*
SD	2.8	6.8	6.8	9.0	4.1	5.3	G-C		
Effort[a]	314.0	405.1	268.8	421.4	356.2	392.4	R-C		
Large young	N = 5		N = 2		N = 3				
Mean	1.8	26.7	0.8	13.5	0.7	25.9	G-R		
SD	1.7	9.8	0.1	1.2	0.3	6.0	G-C		
Effort[a]	45.2	475.2	8.2	149.1	15.0	605.5	R-C		

[a] N = Number of nests sampled, Effort = total observation time (min).

of sessions between Broad-bills and Black-chins. For both the small-young and large-young stages, there were no significant differences among species.

Black-chinned Hummingbirds.—I found no significant differences among stages between Guadalupe and Rucker canyons, except for the small-young stage (Table 2). In this case, sessions and recesses were shorter in Guadalupe Canyon. Comparisons between Guadalupe Canyon and Cliff showed significant differences in the construction and incubation stages. Sessions/recesses were longer in Guadalupe Canyon during construction, whereas they were longer during incubation at Cliff. Between Rucker Canyon and Cliff, significant differences existed between construction and incubation. Construction sessions were longer in Rucker Canyon (recesses did not differ between the two areas), while on/off bouts during incubation were significantly shorter in Rucker Canyon.

Activity Budgets

Nest construction.—Female Broad-billed Hummingbirds spent 59.8% of each hour on the nest, while the remaining 40.2% was spent away

TABLE 3

COMPARISONS AMONG STAGES OF NESTING SHOWING THE PERCENTAGE OF TIME NESTING FEMALE HUMMINGBIRDS SPENT ON AND OFF NESTS AND THE ASSOCIATED NUMBER OF BOUTS (SCALED FOR 1-H INTERVALS)

Stage	Broad-billed Guadalupe	Violet-crowned Guadalupe	Black-chinned Guadalupe	Black-chinned Rucker	Black-chinned Cliff
Construction					
On	59.8	56.4	29.2	28.0	47.6
Bouts	23.4	56.4	14.8	19.0	59.0
Off	40.2	43.6	70.8	72.0	52.4
Bouts	23.0	56.0	14.0	18.4	59.0
Incubation					
On	84.3	76.6	75.0	74.0	76.7
Bouts	2.9	3.0	4.9	4.9	2.7
Off	15.7	24.4	25.0	26.0	23.3
Bouts	2.0	2.6	4.0	4.0	2.0
Small young					
On	—	64.7	36.6	43.7	57.3
Bouts	—	3.8	4.0	2.0	2.9
Off	—	35.3	63.4	56.3	42.7
Bouts	—	3.0	3.9	2.0	2.0
Large young					
On	10.8	3.8	9.0	6.9	3.5
Bouts	3.0	3.0	3.0	5.0	3.0
Off	89.2	96.2	91.0	93.1	96.5
Bouts	3.0	2.5	2.1	4.1	2.2

(Table 3). They averaged 23.4 attentive bouts (mean duration 1.5 min, Table 1) and 23.0 inattentive bouts (mean 1.1 min, Table 1) per hour (Table 3). Violet-crowned Hummingbirds were similar to Broad-bills but they differed from syntopic Black-chins in that the latter spent less time at the nest and had fewer bouts. Black-chins in Rucker Canyon were similar to those in Guadalupe Canyon, whereas those at Cliff were intermediate between these two populations and Broad-bills and Violet-crowns in Guadalupe Canyon (Table 3).

Incubation.—Attentiveness for this stage of the nesting cycle was similar for all species and areas in my study. Black-chins in Guadalupe and Rucker canyons and Violet-crowns spent virtually the same percentage of time on and away from nests, but this was achieved through different strategies (Table 3). Black-chins exhibited a greater frequency of on/off bouts (Table 3), and these were of shorter duration than those of Violet-

crowns (Table 1). Broad-bills spent more time on their nests than either of the above species, were away less, and had fewer bouts (Table 3). Black-chins at Cliff were similar to all other species, although the frequency of on/off bouts was most like Broad-bills (Table 3).

Small young.—In one segment of Guadalupe Canyon, I was able to observe a Violet-crowned nest and a Black-chinned nest simultaneously. The Black-chinned under surveillance was generally present when the Violet-crowned was away and absent when it was present. Additionally, the Violet-crowned was on its nest about the same average time that Black-chins in the canyon were away and vice versa (Table 3). Black-chins at Rucker and Cliff spent more time on their nests and were away for shorter periods than Black-chins in Guadalupe Canyon. Black-chins at all three sites had shorter sessions and longer recesses than Violet-crowns (Table 3).

Large young.—All species in Guadalupe Canyon showed similar attentiveness patterns, although Violet-crowns averaged less time on the nest than Black-chins and Broad-bills (Table 3). Attentiveness in Black-chins in Rucker Canyon was similar to that in this species in Guadalupe Canyon, except that the former had shorter recesses (Table 1 and Table 2) and thus more bouts (Table 3). Black-chins at Cliff differed from those in Guadalupe and Rucker canyons in terms of the number of bouts and in total time spent on and away from nests. In these respects, this population was more like Violet-crowns than other Black-chinned populations.

Feeding young.—The time females spent feeding young did not differ significantly among species or areas. Feeding sessions in Broad-bills averaged 44 sec (N = 13, SD = 19.3), which is the same as in Violet-crowns (N = 46, SD = 18.1). Black-chins in Guadalupe and Rucker canyons had the same average time, which amounted to 51 sec (N = 30, SD = 20.4 and N = 20, SD = 23.2, respectively). The feeding sessions in Black-chins at Cliff averaged 43 sec (N = 29, SD = 16.3).

Diurnal Patterns

Hummingbirds in Guadalupe Canyon.—Attentiveness during incubation was shortest in the morning, longest during mid-day, and intermediate during the evening (Fig. 1). Recesses for all species were longest in the evening, which is the period preceding the nighttime fast. Violet-crowns differed from Broad-bills and Black-chins (morning recesses shortest and intermediate during mid-day) in that their recesses were of intermediate duration during mornings and shortest during mid-day.

Data for Broad-bills during the small-young stage are limited to casual observations, and thus comparisons are restricted to Black-chins and Vi-

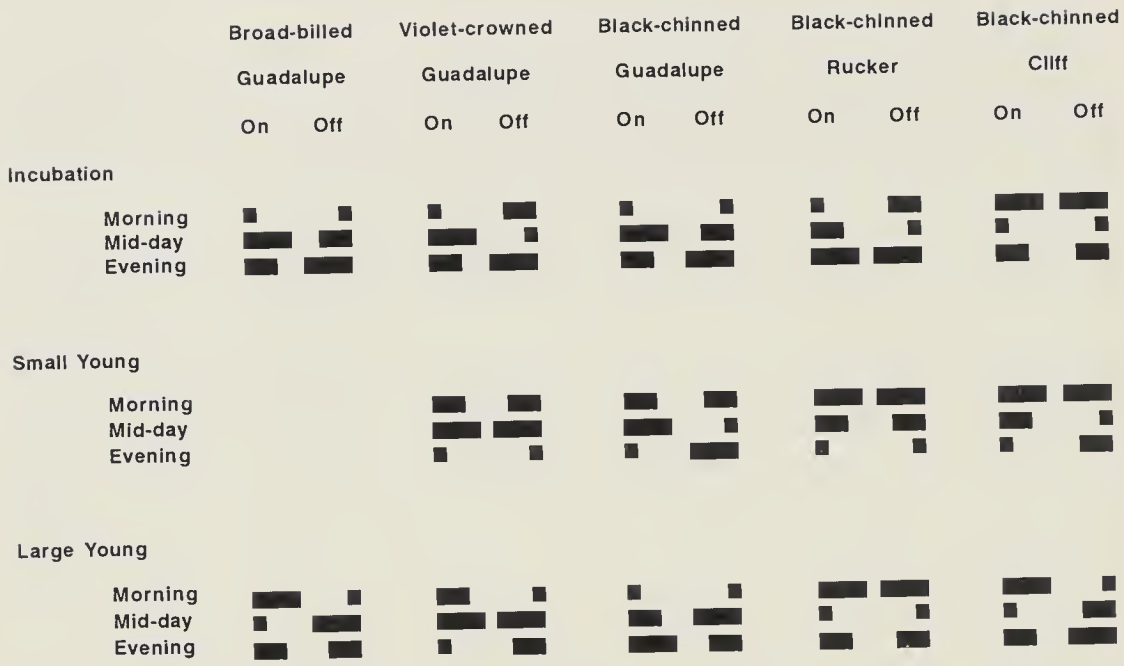

FIG. 1. Diurnal patterns in attentive behavior among species and areas for different stages of nesting; duration of bouts shortest (smallest polygon), duration intermediate in length (medium polygon), and duration longest (largest polygon; bout duration based on morning, mid-day, and evening averages).

olet-crowns (Fig. 1). Sessions were shortest during evening hours, longest during mid-day, and of intermediate length during mornings, which is the first opportunity to renew energy levels following nocturnal fasting. Recesses for both species were of intermediate length during morning hours. They were longest for Violet-crowns during mid-day and for Black-chins during the evening.

When large young were present, each of the three species exhibited a different pattern with regard to the duration of sessions (Fig. 1). However, all species exhibited the same pattern for recesses in that they were shortest in the morning, longest during mid-day, and of intermediate duration during evening periods. Comparisons among species show no other shared patterns *within* stages of nesting, and relatively few patterns were the same when comparisons were made *among* stages (Fig. 1).

Black-chinned Hummingbirds.—Comparisons among areas reveal that a number of patterns were similar in this species (Fig. 1). For example, incubation sessions in Guadalupe and Rucker canyons were shortest during mornings, which was in marked contrast to Cliff where they were longest (response to lower ambient temperature?). Recesses were shortest during mid-day in Rucker Canyon and Cliff, whereas they were longest during evening hours in Guadalupe and Rucker canyons.

The single feature in common among areas was during the small-young

stage (Fig. 1), with sessions shortest during evening hours (the last opportunity to renew energy reserves prior to nocturnal fasting). At Rucker Canyon and Cliff, sessions and recesses were longest during morning hours (first opportunity after the nighttime fast to renew energy levels). Mid-day recesses were of intermediate duration in Rucker Canyon and shortest in Guadalupe Canyon and Cliff.

When large young were present, sessions in Rucker Canyon and Cliff were shortest during mid-day, longest in the morning, and of intermediate duration during evening hours (Fig. 1). In Guadalupe Canyon, sessions were shortest in the morning and longest in the evening. Recesses were shortest during mornings in Guadalupe Canyon and Cliff, but in Rucker Canyon they were longest. Recesses were of intermediate duration in the evening for Guadalupe and Rucker canyons (they were most lengthy at Cliff).

Nest Defense

Females often reacted to intrusions by other animals (even machinery) when these transgressions were into areas near their nests (Table 4). In some instances, this involved scolding or even attack by the female. Disruptions at other times resulted in the female disappearing for a brief period, whereas in other cases they evidenced "curiosity" at the intrusion. Conspecifics were the major cause of nest defense by Black-chins in Guadalupe and Rucker canyons. Black-chins rarely responded in this manner at Cliff, even though in several instances incubating females were within sight of each other. Interspecific intrusions were also the major cause of nest defense in Violet-crowns. In Broad-bills, nest defense was less frequent but it was elicited equally by incursions by conspecifics and other hummingbirds.

DISCUSSION

Diurnal Patterns

The incubation and small-young stages of the nesting cycle were most similar to one another (Table 1). By contrast, the construction and large-young stages had little in common and were each very different from the other two stages. These relationships (or lack thereof) can be interpreted in a number of ways. However, I assume that the similarity between the incubation and small-young stages was due, at least in part, to thermal constraints, small young being somewhat ectothermic after hatching. On the other hand, large young are farther along in their development and thus would not be expected to make the same demands upon the female as developing embryos or small young, which is also true of nest con-

TABLE 4

FACTORS THAT INDUCED FEMALE BROAD-BILLED (BB), VIOLET-CROWNED (VC), AND BLACK-CHINNED (BC) HUMMINGBIRDS TO LEAVE THEIR NESTS[a]

Source of distraction	Distractions/h by area and hummingbird species				
	Guadalupe Canyon			Rucker Canyon	Cliff
	BB	VC	BC	BC	BC
Cooper's Hawk (*Accipiter cooperii*)	—	—	—	0.02	—
American Kestrel (*Falco sparverius*)	—	0.04	0.02	—	—
Broad-billed Hummingbird (*Cynanthus latirostris*)	0.11	0.08	—	—	—
Violet-crowned Hummingbird (*Amazilia violiceps*)	0.17	—	0.02	—	—
Magnificent Hummingbird (*Eugenes fulgens*)	—	—	—	0.08	—
Black-chinned Hummingbird (*Archilochus alexandri*)	0.06	0.19	0.28	0.18	0.02
Hummingbird spp. (Trochilidae)	—	—	0.06	0.02	—
Acorn Woodpecker (*Melanerpes formicivorus*)	—	—	—	0.02	—
Gila Woodpecker (*Melanerpes uropygialis*)	—	—	0.02	—	—
Ash-throated Flycatcher (*Myiarchus cinerascens*)	—	—	0.06	—	—
Brown-crested Flycatcher (*Myiarchus tyrannulus*)	—	—	0.02	—	—
Cassin's Kingbird (*Tyrannus vociferans*)	—	—	0.05	—	—
Thick-billed Kingbird (*Tyrannus crassirostris*)	—	0.08	0.02	—	—
Gray-breasted Jay (*Aphelocoma ultramarina*)	—	—	0.05	—	—
Northern Mockingbird (*Mimus polyglottos*)	—	—	0.02	—	—
Summer Tanager (*Piranga rubra*)	—	0.04	0.05	—	0.02
Black-headed Grosbeak (*Pheucticus melanocephalus*)	—	—	—	0.02	—
Canyon Towhee (*Pipilo fuscus*)	—	—	0.03	—	—
Hooded Oriole (*Icterus cucullatus*)	—	0.04	0.12	—	—
Evening Grosbeak (*Coccothraustes vespertinus*)	—	—	—	0.02	—
Unknown bird species	—	—	0.02	0.04	—
Cattle (*Bos taurus*)	—	0.04	—	—	—
People (*Homo sapiens*)	0.06	—	0.03	0.02	0.06
Bumblebee (*Bombus* sp.)	—	—	—	—	0.02
Pipevine Swallowtail Butterfly (*Battus philenor*)	—	—	0.02	—	—
Unknown	0.06	0.04	—	—	—
Total number of distractions/hour	0.46	0.55	0.89	0.42	0.12

[a] Broad-billed observations based on six nests and 17.5 h of direct observation; Violet-crowned observations based on five nests and 26.1 h of direct observation; Black-chinned observations for Guadalupe Canyon based on 25 nests and 67.4 h, for Rucker Canyon 11 nests and 50.5 h, and for Cliff 10 nests and 47.7 h of direct observation.

struction. I have confined my discussion of diurnal patterns in attentive behavior (Fig. 1) to the incubation and small-young stages and, in turn, to hummingbirds in Guadalupe Canyon. This was done to avoid the confounding effects of differing selective pressures during other stages in the nesting cycle and among geographic areas.

Incubation.—A consistent pattern of nest attentiveness relative to time of day was evident among the hummingbirds in Guadalupe Canyon (Fig.

1). Morning sessions were shortest, which may well have resulted from the needs of females to feed themselves after the nocturnal fast, balanced against meeting the requirements of the developing embryos. Mid-day sessions were longest during incubation when temperatures were highest (average ambient temperatures [shade] of 32.6°C [SD = 0.8], with extremes of 31 to 38°C). This is contrary to many published expectations (e.g., Kendeigh 1952, 1963; von Haartman 1956; White and Kinney 1974) which suggest the existence of an inverse correlation between temperature and attentiveness. The intermediacy of evening sessions (Fig. 1) and the duration of evening recesses (longest of day for each species) are believed to represent periods of crop-filling anticipatory to evening fasting. Such an explanation is consistent with the feeding behavior of both free-living and captive hummingbirds (Beuchat et al. 1979, Wheeler 1980, Powers and Nagy 1988, Tiebout 1989, Powers 1991).

My findings regarding mid-day sessions might be interpreted as females shading their eggs (see Wolf 1964, Vleck 1981). However, female posture on the nest, and the fact that nests were not in direct sunlight, does not support this interpretation. Instead, the results might indicate that females remained on the nest as a way of minimizing energy expenditures or be a strategy for heat dissipation without excessive water loss (see Ricklefs 1971, 1974; Calder 1974). Another possibility is that females remained at the nest to foil ectothermic predators (e.g., snakes), many of which are most active during the warmer portion of the day.

Small young.—Attentive patterns of Violet-crowned and Black-chinned hummingbirds generally were similar (Fig. 1; data for Broad-bills lacking). Afternoon sessions were longest, which strengthens the argument that temperature and attentiveness were not inversely related. The intermediacy of sessions in both species during morning sessions contrasts with that for incubation when sessions were shortest. This may indicate that newly hatched young either (1) required more parental care than developing embryos or (2) that females expended less nighttime energy and could "afford" to remain at the nest longer. That evenings were used to "tank up" prior to fasting is supported in Black-chins by the fact that sessions were shortest and recesses longest during this stage (same pattern as in incubation).

Violet-crowned Hummingbird attentiveness during the evening period differed from that of Black-chins, being marked by the shortest sessions and recesses of the day. When the female was not at her nest, she was often perched in sight of it for relatively long periods. This might suggest that this period was not important for replenishing nectar supplies. However, plentiful and nearby Parry agaves (*Agave parryi*) were beginning to produce large quantities of nectar at this time (Baltosser 1989b), thus

providing an abundance of food. This fact, plus the dominance of the Violet-crowned over Black-chinned and Broad-billed hummingbirds (Baltosser 1989b), may well have allowed the former to "refuel" more quickly (see Howell and Dawson 1954 for pertinent discussion).

Attentiveness Strategies

In most birds in which only one sex tends the eggs (excluding certain nidifugous species), the eggs are incubated 60–80% of the daylight hours (Skutch 1962). These levels of attentiveness curtail foraging, and under some circumstances, incubating birds may have difficulty finding enough food to maintain themselves (Skutch 1962, Walsberg 1983, Williams 1993). When levels fall below 60%, hatching may be retarded. However, an increase in levels above 70–80% does not necessarily shorten the incubation period (Skutch 1962).

In my study, the percentage of time hummingbirds covered their eggs during incubation was similar among the three species (Table 3). Black-chins and Violet-crowns in Guadalupe Canyon were very similar, as was the case for Black-chins among areas ($\bar{x}$ = 75.2%, SD = 1.4). However, despite the uniformity in overall time spent at the nest, the way in which it was partitioned varied among species. For example, Broad-billed and Violet-crowned hummingbirds had relatively few on/off bouts, which were relatively longer (Table 1). By contrast, Black-chinned Hummingbirds had shorter sessions and recesses (at least for Guadalupe and Rucker canyons) which resulted in more bouts.

Disruptions

Nest attentiveness during incubation and care of small young is clearly affected by what might be termed "intrinsic" considerations, e.g., thermoregulation, self-maintenance, and feeding of young. In addition, "extrinsic" considerations also affect attentiveness, the most important of which is intrusions into the nest area by other animals. Whether the intruders are potential competitors, predators, or neutral in intent, female hummingbirds can respond in one of two ways: passively or actively. Two opposing tendencies are thus exhibited by female hummingbirds while sitting on their nests: (1) to passively reduce interactions centered around the nest and (2) to actively defend the nest against intruders (Wolf and Wolf 1971, present study).

Comparative material is virtually lacking, but in the Purple-throated Carib (*Eulampis jugularis*), Wolf and Wolf (1971) found that nest defense was strongest against birds that posed the greatest source of danger; it declined as this potential diminished. Female Caribs often, though not inevitably, responded to intrusions by leaving the nest in pursuit. Large

passerines were responsible for 51% of all disruptions, followed in descending order by small passerines (29%), conspecifics (12%), and other hummingbirds (9%).

Responses similar to those of the Purple-throated Carib were seen in my study when females were faced with intrusions by animals near their nests. However, compared to the Caribs, intrusions by conspecifics and other hummingbirds played a more prominent role (Table 4). Conspecifics were the major single source of disruption for Black-chins in both Guadalupe and Rucker canyons, amounting to 34% and 43%, respectively. The impact of other hummingbirds on this species was less in both areas, being only 9% and 24%, respectively. In Guadalupe Canyon, the impact of all other species on Black-chins was 57%, of which most were attributable to large passerines (Table 4). For Black-chins in Rucker Canyon, 34% of all interactions resulted from other non-hummingbird species, primarily large passerines. Black-chins were the only nesting hummingbird at Cliff, and despite the presence of an occasional migrant Broad-tailed (*Selasphorus platycercus*), Rufous (*Selasphorus rufus*), or Calliope (*Stellula calliope*), were not disrupted by these hummingbirds. Overall, disruptions at this site were minimal, with 50% being generally attributable to human interference.

Conspecific intrusions were not a factor for Violet-crowns, as the species was relatively rare and nests were widely dispersed. However, intrusions by Black-chinned and Broad-billed hummingbirds accounted for 50% of all cases in which Violet-crowns left their nest. Larger passerines were the other major source of disruption, accounting for 29% of the intrusions to which Violet-crowns responded. In Broad-billed Hummingbirds, conspecific intrusions accounted for 25% of the aggressive responses by this species. In addition, defense of the nest against other hummingbirds accounted for 50% of the responses of nesting Broad-bills.

The potential impact of intrusions around the nest can be examined by noting how frequently females left their nests and their fledging success. Comparisons of species nesting in Guadalupe Canyon show a significant inverse correlation between these parameters ($r = -0.996$, df = 1, $P < 0.05$), based on 6663 minutes (111 h.) of intensive observation at 36 nests (Baltosser 1986b). On average, fledging success for Black-chins was 44%, with nearly one intrusion/hour (Table 4), 60% for Violet-crowns with just over 0.5 intrusions/hour (Table 4), and 66.7% for Broad-bills with just under 0.5 intrusions/hour (Table 4). Black-chinned nesting success vs intrusion rate was not significantly correlated in Rucker Canyon or at Cliff.

Comparing attentiveness at successful nests vs those that were unsuccessful is another way of assessing the impact of intrusions around the nest. Because of limited sample size, this is possible only for Black-

chinned Hummingbirds, and then only during incubation (stage with greatest mortality, see Baltosser 1986b). Attentiveness for Black-chins in Guadalupe Canyon that fledged averaged 75% (SD = 7.4, Range = 66–84%) and unsuccessful nests averaged 67% (SD = 10.7, Range = 50–81%). In Rucker Canyon, attentiveness was reversed, i.e., percentages for nests that fledged were lower ($\bar{x}$ = 71%, SD = 10.4, Range = 61–84%) than those which failed ($\bar{x}$ = 76%, SD = 3.9, Range = 71–81%). Black-chins at Cliff that were successful had greater attentiveness ($\bar{x}$ = 77%, SD = 7.2, Range = 68–86%) than those that were unsuccessful ($\bar{x}$ = 71%, SD = 5.8, Range = 67–75%).

Attentiveness in the Trochilidae

The data presented in this paper on nest attentiveness during incubation are compared with those on other hummingbirds in Table 5. In addition to studies already cited, this table includes data from Orr (1939), Skutch (1951, 1958, 1964, 1967), Calder (1971, 1975), Smith et al. (1974), and Montgomerie and Redsell (1980). Data are arranged by species and by the primary area in which each nests (i.e., temperate, subtropical, and tropical latitudes). Collectively, these data show that hummingbirds are similar in incubation attentiveness regardless of species and latitude. This suggests the existence of a fixed requirement for this stage of reproduction, which hummingbirds have been able to meet effectively throughout a wide variety of nesting habitats (Vleck 1981).

Aside from the present study, comparative data for other stages of the nesting cycle are generally unavailable for most hummingbirds. However, comparisons are possible based on Wolf and Wolf's study (1971) of the Purple-throated Carib and that of Bené (1940) on the Black-chinned Hummingbird. Female Caribs with small young spent 59.5% of each hour at the nest, compared to 57–59% for Black-chins in the study by Bené. These percentages are similar to my findings on Violet-crowned Hummingbirds in Guadalupe Canyon and nearly identical to Black-chins at Cliff (Table 2). Attentiveness in Black-chins in Guadalupe Canyon at this stage was only 36.6%, while that in Rucker Canyon was 43.7%.

For nests having large young, data from Wolf and Wolf (1971) shows attentiveness to average 8.5% (range 5.7–13.4%), based on three days of observation. This average is nearly the same as the 9% obtained for Black-chins by Bené (1940), and these are very similar to the 10.8% in Broad-bills and 9.0% in Black-chins I found in Guadalupe Canyon. In contrast, my figures were 3.8% for Violet-crowns, 3.5% for Black-chins at Cliff, and 6.9% for Black-chins at Rucker Canyon.

Wolf and Wolf (1971) found that feeding bouts for young in Purple-throated Caribs averaged 38 sec (SD = 11). This is similar to the 44 sec

TABLE 5

COMPARISONS AMONG TEMPERATE, SUBTROPICAL, AND TROPICAL NESTING HUMMINGBIRDS SHOWING UNIFORMITY IN ATTENTIVENESS DURING INCUBATION

Species of hummingbird	Average length (min.)		Percent attentive	Source
	Sessions	Recesses		
Temperate				
Black-chinned Hummingbird	6.3	2.3	70	Vleck 1981
(*Archilochus alexandri*)	8.9	3.9	74	Baltosser, present study
	17.1	7.0	77	Baltosser, present study
	9.1	3.8	75	Baltosser, present study
Anna's Hummingbird	14.5	6.4	69	Calder 1975
(*Calypte anna*)	15.5	2.8	84	Howell and Dawson 1954
	8.5	2.2	79	Smith et al. 1974
	8.1	3.0	75	Vleck 1981
Costa's Hummingbird				
(*Calypte costae*)	15.8	2.4	83	Vleck 1981
Broad-tailed Hummingbird	7.7	2.1	78	Calder 1975
(*Selasphorus platycercus*)	—	—	72	Montgomerie and Redsell 1980
Allen's Hummingbird				
(*Selasphorus sasin*)	4.6	1.4	77	Orr 1939
Calliope Hummingbird				
(*Stellula calliope*)	7.3	2.0	77	Calder 1971
Subtropical				
Violet-crowned Hummingbird				
(*Amazilia violiceps*)	15.1	5.6	77	Baltosser, present study
Broad-billed Hummingbird				
(*Cynanthus latirostris*)	17.3	4.7	84	Baltosser, present study
White-eared Hummingbird				
(*Hylocharis leucotis*)	9.1	4.0	70	Skutch 1962
Tropical				
Violet Sabrewing (*Campylopterus hemileucurus*)	42.8	24.0	64	Skutch 1967
Purple-throated Carib				
(*Eulampis jugularis*)	—	—	69	Wolf and Wolf 1971
Violet-headed Hummingbird				
(*Klais guimeti*)	40.6	15.2	73	Skutch 1958
White-crested Coquette				
(*Lophornis adorabilis*)	11.9	6.4	64	Skutch 1962
Scaly-breasted Hummingbird				
(*Phaeochroa cuvierii*)	20.9	6.9	76	Skutch 1962
Little Hermit	24.7	11.7	67	Skutch 1951
(*Phaethornis longuemareus*)	40.7	16.4	71	Skutch 1962
	36.9	15.3	70	Skutch 1964

that I found in Broad-billed and Violet-crowned hummingbirds and to the 43 sec in Black-chins at Cliff. Black-chins in Guadalupe and Rucker canyons had bouts that averaged 51 sec, which is similar to what can be deduced for this species from Bené (1940).

SUMMARY AND CONCLUSIONS

Hudson (1920) and Woods (1927) were among the first to comment on the uniformity of general life-history traits among hummingbirds. Pitelka (1942) noted that this degree of uniformity is perhaps as extreme as that in any group of similar taxonomic rank. The data from the present study, coupled with those cited within, demonstrate considerable uniformity in nest attentiveness within the Trochilidae. This is best exemplified during incubation, but evidence of behavioral consistency is shown in all stages. This is remarkable, given the disparity among the species and latitudes from which comparative data were obtained.

The three hummingbird species that I studied in Guadalupe Canyon exhibited similar attentiveness during the incubation and small-young stages, i.e., stages of development when embryos and young were perhaps most vulnerable to thermal fluctuations. Anticipatory feeding was common and often characterized the behavior of female hummingbirds during hours immediately preceding the nocturnal fast. During morning hours when ambient temperatures were lowest, the need to replenish energy reserves depleted during the night was apparent in the behavior of nesting females. However, presumably because of thermoregulatory needs of embryos and newly-hatched young, attentive patterns seem to reflect a compromise between the female's needs and those of her brood.

Lengths of sessions and recesses can provide insight into resource availability and the competitive environment among hummingbirds. Factors that increase the comings and goings from a nest beyond those essential for self-maintenance, incubation, or the feeding of young may play a critical role. Success vs failure may hinge on extrinsic items that increase the number of unscheduled departures from the nest. For example, escalating the number of departures from a nest may increase predation through nest betrayal (Skutch 1949, 1962). Low constancy during incubation may also result in the death of embryos and young (e.g., Grant 1982) or prolong incubation (Pienkowski 1984) and, thereby, the risk of nest predation (Byrkjedal 1985).

Correlation is not the strongest form of inference (e.g., see Eberhardt 1970, Romesburg 1981), but results such as mine can provide valuable insights into biological processes. Given the potential data to be gained by focusing on interactions at the nest, it is surprising that more studies have not pursued this line of investigation. My research and that con-

ducted by Wolf and Wolf (1971) demonstrate the need to investigate the extent to which female hummingbirds are induced by outside forces to leave their nests. The consequences of such disruptions (including frequency and duration) are potentially great and are a much overlooked aspect of the breeding biology of hummingbirds.

ACKNOWLEDGMENTS

I thank R. J. Raitt and J. P. Hubbard for their help throughout all aspects of this study. Appreciation is extended to S. M. Russell, F. N. White, W. M. Shepherd, C. R. Blem, and three anonymous reviewers for their guidance and encouragement. I am indebted to the Magoffin and Hadley families of Guadalupe Canyon, the personnel of the Coronado National Forest in Rucker Canyon, and the Hunt family at Cliff. I also am extremely grateful to Mr. and Mrs. W. W. Baltosser, my wife Ginger, and my daughter Dianna. This work was supported in part by the New Mexico State Univ. Dept. of Biology, the New Mexico Dept. of Game and Fish (contract No. 519-68-06), and Chapman Memorial grants (61462, 84472, and 110115) from the American Museum of Natural History.

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Wilson Bull., 108(2), 1996, pp. 246–267

SEASONAL POPULATION SURVEYS AND NATURAL HISTORY OF A MICRONESIAN BIRD COMMUNITY

Robert J. Craig

Abstract.—I replicated quarterly population surveys of landbirds on Saipan, Mariana Islands at two environmental scales: habitat specific and island-wide. I determined population densities and the degree of seasonal fluctuation in counts to compare densities in native vs disturbed habitat and to observe whether populations exhibited characteristics of those at either saturation or below saturation densities. I also gathered new data on the natural history of largely unknown species. For seven of the nine forest birds examined, interseasonal census variation was greater than intra-seasonal variation, suggesting that most of the species undergo seasonal shifts in population or breeding status (the latter case was indicated for four forest species). The principal difference uncovered between the two census scales was that the Micronesian Honeyeater (*Myzomela rubrata*) was relatively uncommon in native forest but regular on island-wide counts. Otherwise, forest species showed numerous similarities in count trends at both scales. However, habitat-specific data showed that for many species, counts and computed densities were greater in native forest than in disturbed habitat. Independent density assessment (based on a new procedure) for the Bridled White-eye (*Zosterops conspicillatus*) was of the same order of magnitude as that obtained through censusing. The densities reported here, particularly for the Rufous Fantail (*Rhipidura rufifrons*), Bridled White-eye, and Golden White-eye (*Cleptornis marchei*), are among the highest ever reported for birds (>1900/km^2) and are almost certainly at habitat saturation. Interspecific competition is expected in such a case, and interspecific aggression was prevalent, particularly among ecologically similar species. *Received 27 April 1995, accepted 1 Dec. 1995.*

Land birds of the Mariana Islands, Micronesia have received limited, mostly qualitative study (e.g., Marshall 1949, Baker 1951, Pratt et al. 1987, Reichel and Glass 1991), and the quantitative ecology of most species remains unknown. Jenkins (1983) reviewed aspects of the natural history of the now mostly extinct (Savidge 1987) avifauna of the southernmost island of Guam, and Engbring et al. (1986) reported population estimates, based on one survey, for Rota, Aguiguan, Tinian, and Saipan. Quantitative scrutiny has been given only to the Nightingale Reed-Warbler (*Acrocephalus luscinia*) (Craig 1992a) and Bridled White-eye (*Zosterops conspicillatus*) and Golden White-eye (*Cleptornis marchei*) (Craig 1989, 1990).

The island of Saipan presently has the most diverse, albeit meager, assemblage of land birds in the Marianas. It consists of three medium-sized predators, the Yellow Bittern (*Ixobrychus sinensis*), Collared Kingfisher (*Halcyon chloris*) and Nightingale Reed-warbler; two herbivores,

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the Mariana Fruit-Dove (*Ptilinopus roseicapilla*) and White-throated Ground Dove (*Gallicolumba xanthonura*); four omnivores, the Micronesian Megapode (*Megapodius laperouse*), Micronesian Starling (*Aplonis opaca*), Golden White-eye, and Bridled White-eye, a nectarivore, the Micronesian Honeyeater (*Myzomela rubrata*); and two small insectivores, the Island Swiftlet (*Aerodramus vanikorensis*) and Rufous Fantail (*Rhipidura rufifrons*). Most of these species, or at least their local subspecies, are endemic to the Marianas or Micronesia. Prehistorically, perhaps twice as many species were present (Steadman 1992). Two other species, the Javanese Turtle Dove (*Streptopelia bitorquata*) and Eurasian Tree Sparrow (*Passer montanus*), are present but not native.

This study reports replicated, quarterly population surveys I made of these species on Saipan. They were made at two environmental scales, habitat specific and island-wide, to determine population densities and the degree of fluctuation in populations or breeding activity. Because all species are nonmigratory, I hypothesized that populations might build to the maximum density sustainable by available resources and that little fluctuation in densities generally occurs. I also gathered new natural history data on many species.

STUDY AREAS AND METHODS

Habitats.—The island of Saipan is predominantly a raised coral island 22 km long and 3–10 km wide. It has a climate with uniform temperatures but seasonal rainfall. Typically, and during this study, the dry season is December–June and the wet season is July–November. Reduced rainfall, establishment of easterly trade winds (Young 1989), and decline in flowering, fruiting, and growth by certain native tree and vine species characterize the dry season. During the wet season rain increases, particularly August–September, trade winds break down (Young 1989), and beginning in the late dry season, many native trees and vines flower and fruit. Typhoons are frequent during the latter half of the year and exert a strong influence on the structure of natural habitats (Fosberg 1960).

Much of Saipan likely was once forested, particularly on limestone soils (Fosberg 1960). Such limestone forest is relatively xerophytic except at the highest elevations (ca 300–466 m), where near cloud forest conditions prevail. This forest is typically dense, with a canopy dominated by two widespread Indo-Pacific trees, *Pisonia grandis* and *Cynometra ramiflora*, and understory of mostly *C. ramiflora* and the Mariana endemic *Guamia mariannae* (Craig 1992b). Other natural habitats, including ravine forest, swordgrass (*Miscanthus floridus*) savannah (both occurring on exposures of volcanic soil), mangrove swamp, freshwater swamp, reed (*Phragmites karka*) marsh, strand forest, and coastal scrub are also present. Combined, native habitats presently cover roughly 30% of the island.

The remainder of Saipan's natural habitats have developed on disturbed sites. Level areas are largely abandoned agricultural lands (Fosberg 1960) vegetated by elephant grass (*Pennisetum purpureum*) meadows, and tangantangan (*Leucaena leucocephala*) thickets. Secondary forests of introduced species, particularly sosuge (*Acacia confusa*), white monkeypod (*Albizia lebbeck*), and flametree (*Delonix regia*) are also common, as are areas of "agriforest" (Engbring et al. 1986) where trees such as coconut (*Cocos nucifera*) and mango (*Mangifera indica*) are frequent.

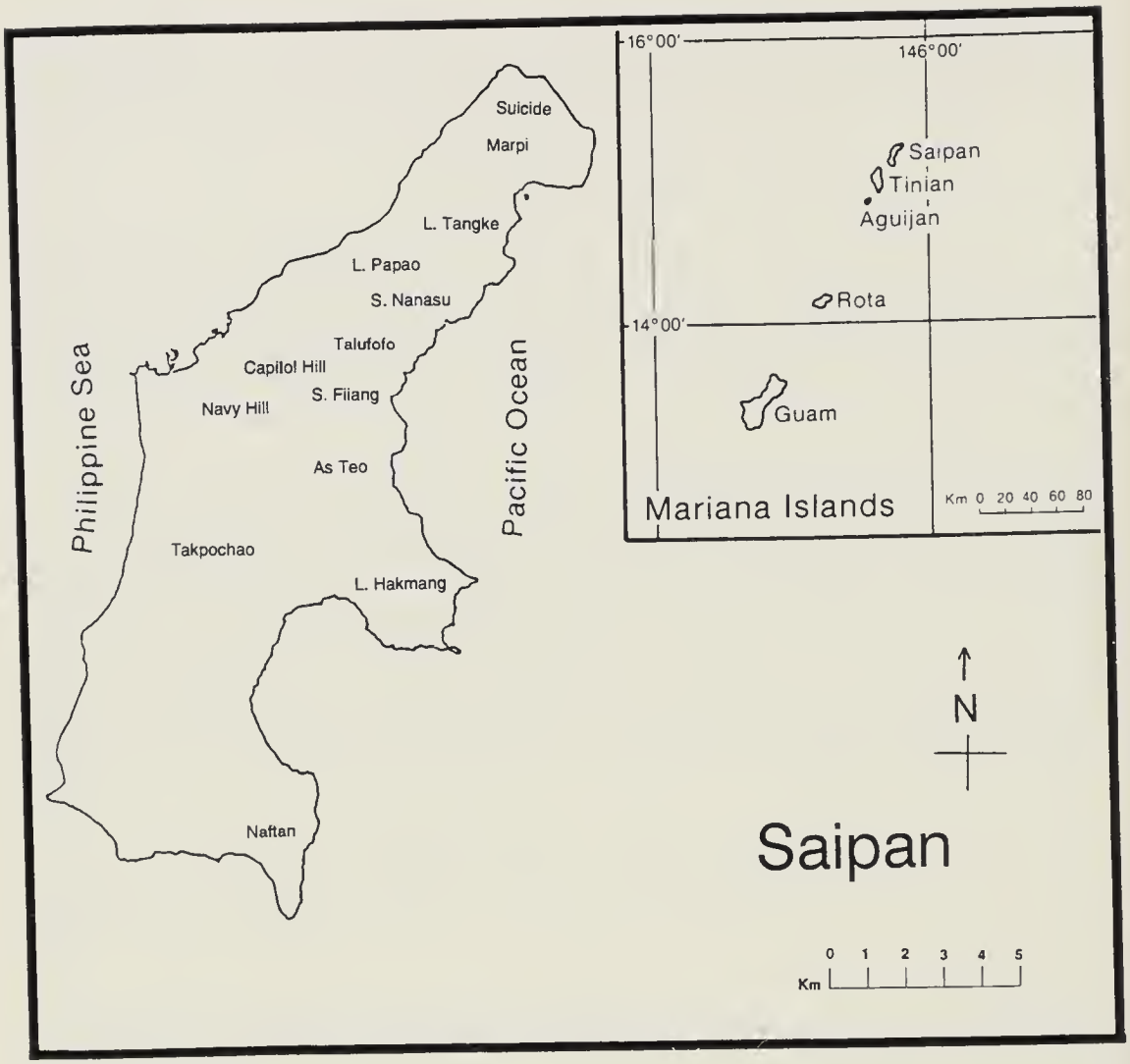


FIG. 1. The island of Saipan, Mariana Islands, with names of principal locations mentioned in this study.

Bird censuses.—I performed two types of bird censuses: variable circular plot (Reynolds et al. 1980) surveys and U.S. Fish and Wildlife Service breeding bird surveys. The former were conducted in limestone forests of the Marpi region of northern Saipan (Fig. 1). I censused two separate locations. The first was an old Japanese hiking trail, the Banadero Trail, located along the west slope of a steep escarpment known as Suicide Cliff. The second was a modern hiking trail along the Laderan Tangke cliffline. Marpi is characterized by steep limestone escarpments with the most extensive native forest remaining on the island. The breeding bird survey traversed the island from north to south and covered a variety of habitats.

I used the variable circular plot (VCP) technique, chosen because of its utility in rough tropical terrain (Scott et al. 1986), to survey 15 points each at the two census routes (30 total points). Based on the frequency with which birds provided cues, I established count periods of 8 min/station. Points were 100 m apart except at Laderan Tangke, where one set of stations was placed 200 m apart and another 300 m apart to avoid disturbed habitat. At each point, I recorded all birds seen or heard and estimated the distance of each bird from

TABLE 1

DETECTION DISTANCES (M) USED FOR COMPUTING POPULATION ESTIMATES OF BIRDS IN DISTURBED HABITATS, LIMESTONE FOREST, AND IN THE 1982 SURVEY (ENGBRING ET AL. 1986)

Species	Disturbed habitats		Limestone forest		1982
	Distance	N	Distance	N	Distance
Micronesian Megapode	0	0	80	32	105
White-throated Ground Dove	—[a]	—	20	51	80
Mariana Fruit Dove	70	20	50	155	159
Collared Kingfisher	70	56	50	283	193
Rufous Fantail	20	127	10	706	58
Nightingale Reed-warbler	50	34	0	0	87
Micronesian Starling	40	30	15	220	66
Micronesian Honeyeater	25	54	15	52	58
Bridled White-eye	15	590	10	2291	33
Golden White-eye	20	70	10	615	42

[a] Because an insufficient sample was available, the distance estimate for limestone forest was used in computations.

the point. Censuses began at sunrise and were conducted under conditions of minimal rain and low wind (although wind averaged higher in the dry season). Practice censuses were conducted in October 1990, and censuses were made at quarterly intervals thereafter in January, April, July, and October, 1991–1992. Replicate data were, therefore, available for each year and for the wet and dry seasons. I also made five replicate censuses each at the two routes from late April to mid-May 1993 in order to assess within-season variation in counts.

Although I attempted to calibrate distance estimates by placing plastic flagging at 10, 15, and 20 m intervals (the maximum distance easily visible in limestone forest) from selected census points and by walking from the point to distantly vocalizing birds during practice censuses, distances were difficult to estimate (Table 1). Indeed, correctly estimating the distance to the roughly 15 birds/census point, under varying conditions of topography, vegetation density, and orientation of the bird to the point, even for an observer with 20 years of censusing experience, seemed an unrealistic expectation. Hence, population densities derived from such estimates are of limited accuracy. I report computed densities and make independent assessments of their utility but use direct counts for many analyses and recommend that future studies compare counts rather than densities when possible.

In addition to these regularly performed surveys, I employed the VCP procedure at three disturbed sites to provide data comparable with those for native forest. Using the same procedures outlined above (except that points were 150 m apart to improve sampling independence in habitats in which birds could be detected farther), I censused 25 points at Laderan Hakmang (Kagman), 17 points at Sabanan Fiiang, and 17 points at Mt. Takpochao (Tapotchau) in March 1993. Laderan Hakmang, the site of a former World War II fighter field complex, is presently a xeric mosaic of meadows, tangantangan thickets, and scattered introduced and native tree species. Sabanan Fiiang, formerly a World War II hospital site, is similarly xeric and largely overgrown by tangantangan and scattered introduced and native trees, particularly ironwood (*Casuarina equisetifolia*). The Mt. Takpochao area, at least in

part a pre-war coffee (*Coffea arabica*) plantation (ca 300 m elevation), is a mesic mosaic of meadows, swordgrass savannah, thickets, and copses of native forest.

The breeding bird survey involved censusing for 3 min at each of 50 roadside stops placed 0.8 km (0.5 mi) apart. Counts began 15 min before sunrise on days with low wind and little rain, and all birds seen or heard to 0.4 km away were recorded. Because the quality of back roads on Saipan is poor, the entire survey took ca. 4.5–5 h to complete. Moreover, the limited availability of back roads necessitated breaking the route into two segments (after station 23) in order to traverse the entire island. Surveys also were conducted quarterly in 1991–1992.

Additional observations.—to investigate additional aspects of avian populations and social systems, I mist netted and color banded small passerines in the Marpi native forest and at Capitol Hill. This second site facilitated study of the Micronesian Honeyeater which was uncommon in limestone forest but common in suburban settings.

Intensive banding of Bridled White-eyes at Capitol Hill provided an assessment of population densities independent of those obtained through bird censuses. I banded white-eyes intermittantly from February 1992 to June 1993, and in February and May 1993, I recorded the proportion of banded vs unbanded birds present within a 50 m radius of the banding site. To determine population distribution, in May 1993 I also assessed the proportions of banded vs unbanded birds at 50 m intervals to 300 m from the banding site.

I made incidental observations on all Saipan land birds throughout my investigations. I paid particular attention to occurrences of interspecific aggression, and I assessed intraspecific aggression by playing back recorded songs to selected species. Data on breeding, foraging, and microhabitat use also were gathered. From 1988 to 1993, I made additional observations on the nearby Mariana Islands of Tinian (4 d), Rota (69 d), and Aguiguan (6 d).

Analysis.—I used the procedure described by Scott et al. (1988) and followed by Engbring et al. (1986) to compute population densities.

For two loudly vocal and wide ranging species, the Mariana Fruit Dove and Collared Kingfisher, VCP census points 100 m apart were inadequate to ensure that observations from each point were independent. For these species, I computed population densities based on 16 alternate census points (at least 200 m apart). Micronesian Megapodes also were detectable at long distances, but because they were sedentary and rare, I was able to distinguish the locations of all individuals encountered.

To obtain independent population estimates for the Bridled White-eye, I employed the Jolly-Seber procedure (Tanner 1978) to analyze capture-recapture data from banding operations. In addition, I used the Lincoln-Peterson index (Tanner 1978) to evaluate populations based on the relative proportions of banded and unbanded birds observed directly around (to 50 m) the banding site (the region assumed to include intersections of home ranges of all birds banded). An assumption of the Jolly-Seber procedure, random sampling of banded and unbanded members of the population, may not have been met because previously captured birds might become net shy. Moreover, the Lincoln-Peterson index requires that no recruitment occur during the study period, an assumption not met during the extended study period. Hence, population estimates based on both methods, particularly the latter, are likely inflated.

To compute population densities, P, from the above indices, I employed data gathered on the dispersion of marked birds from the banding site. I developed a relation using the number of birds with home ranges intersecting the banding site (N) as generated from the two methods above, the area (A) of each of i zones radiating from the banding site at 50 m intervals, the multiple (a_i) of the basal zone (0–50 m from the banding site) area (A_1) of each A_i and the proportion of birds banded in each of these areas (p_i):$P = N/\Sigma_i^i(a_i p_i)$. P was converted to birds/ha by dividing it by the area of the basal zone, 7853 m^2.

TABLE 2

COMPARATIVE COUNTS OF BIRDS (BIRDS/10 STATIONS) FOR 1991–1992 (LIMESTONE FOREST), THE 1993 SURVEY OF DISTURBED SITES, AND THE 1982 SURVEY (ENGBRING ET AL. 1986)

Species	Limestone forest		Disturbed sites	1982 survey
	1991	1992		
Micronesian Megapode	1.0	1.3	—	0.2
Yellow Bittern	—	—	0.2	0.6
White-throated Ground Dove	1.7	2.1 (2.8)[a]	0.7	0.6
Mariana Fruit Dove	5.9 (5.6)[b]	5.9 (6.8)[a] (7.0)[b]	3.6	20.0
Collared Kingfisher	10.6 (12.5)[b]	10.3 (12.3)[b]	10.0	13.6
Rufous Fantail	25.3	28.4	23.0	45.0
Nightingale Reed-warbler	—	—	6.1	11.8
Micronesian Starling	8.5	7.5	5.4	4.7
Micronesian Honeyeater	2.0	2.3	9.8	22.6
Bridled White-eye	87.3	88.7	107.1	77.0
Golden White-eye	22.1	23.9	12.5	30.4

[a] April counts of species with seasonal shifts in calling frequency.
[b] Based on 16 stations spaced 200 m apart.

SPECIES ACCOUNTS

Micronesian Megapode.—Believed to have become extinct on Saipan after the early 1930s, it was rediscovered in 1978 by Pratt et al. (1987). This present population, estimated at 25–50 by Glass and Aldan (1987) is suspected to be descended from birds brought to Saipan from more northern Mariana islands by island inhabitants (Engbring et al. 1986). During this study, I estimated 14 birds to be present in native forests (and occasionally in adjacent tangantangan thickets) of the Marpi region. In 1989 I also heard a bird farther south at Laderan Papao, although I found none there in later years. Despite intensive surveys, I located none at Naftan Point, the southernmost point on Saipan, where Glass and Aldan (1987) previously reported individuals. Hence, populations are likely declining. Both direct counts (Table 2) and density estimates (Table 3) for limestone forest were greater than those recorded in 1982 by Engbring et al. (1986), but the present VCP transects overlapped the only remaining range of the species on Saipan, whereas Engbring et al. (1986) surveyed all habitats throughout the island.

No firm evidence of breeding by this endangered species is known from Saipan. However, in 1991 I located the possible remains (soil and rotting vegetation) of an old nest mound in the Marpi forest, similar in dimensions to those which I have observed in interior forests of the Palau Islands (where a different subspecies occurs). Glass and Aldan (1987)

TABLE 3

COMPARATIVE 1991–1992 DENSITY ESTIMATES (BIRDS/KM^2) FOR BIRDS OF LIMESTONE FOREST, THE 1993 SURVEY OF DISTURBED SITES, AND THE 1982 SURVEY (ENGBRING ET AL. 1986)

Species	Limestone forest		Disturbed sites	1982 survey
	1991	1992		
Micronesian Megapode	2	3	—	1
White-throated Ground Dove	58	72	24	2
Mariana Fruit Dove	27 (26)[a]	27 (32)	11	25
Collared Kingfisher	43 (51)	42 (50)	26	11
Rufous Fantail	2160	2423	647	456
Micronesian Starling	403	356	48	32
Micronesian Honeyeater	123	138	205	203
Bridled White-eye	5904	5994	3992	2221
Golden White-eye	1935	2095	390	532

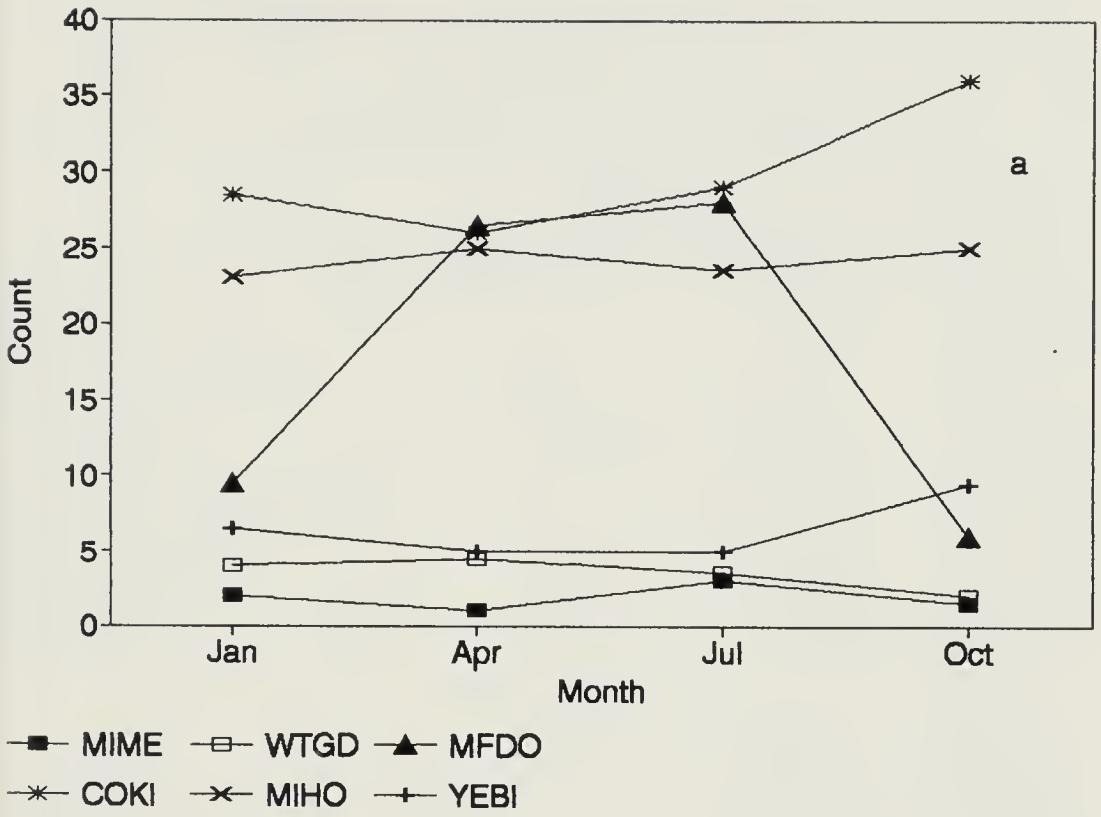
[a] Numbers in parentheses are population estimates based on 16 stations 200 m apart.

suspected a peak in calling (and breeding activity) in January, but in 1991 both limestone forest and island-wide surveys showed a calling peak in July (Figs. 2A, 3A), the month in which I saw two birds engaging in apparent courtship chases (the birds otherwise foraged together and showed no evidence of aggression). This pattern was not repeated in 1992, although replicate counts performed in April 1993 (Table 4) suggested that census variation between seasons was greater than that within a season. Individuals or pairs were sedentary, responded vigorously to playback, and appeared to defend all-purpose territories. Birds could be found in the same areas even between years, although during the study period they invaded new locations on two occasions, thus providing evidence for either territory relocation or reproduction.

Baker (1951) reported that the Micronesian Megapode is omnivorous, although field observations on foraging are virtually nonexistent. I recorded feeding only once, when I observed an individual capture an insect. Foraging birds generally scratched leaf litter with the feet and, at least occasionally, scratched alternately with one foot and then the other.

→

FIG. 2. Mean 1991–1992 population trends of land birds for island-wide counts. (A) MIME—Micronesian Megapode, WTGD—White-throated Ground Dove, MFDO—Mariana Fruit Dove, COKI—Collared Kingfisher, MIHO—Micronesian Honeyeater, YEBI—Yellow Bittern; (B) RUFA—Rufous Fantail, MIST—Micronesian Starling, BWEY—Bridled White-eye, GWEY—Golden White-eye, NRWA—Nightingale Reed-warbler.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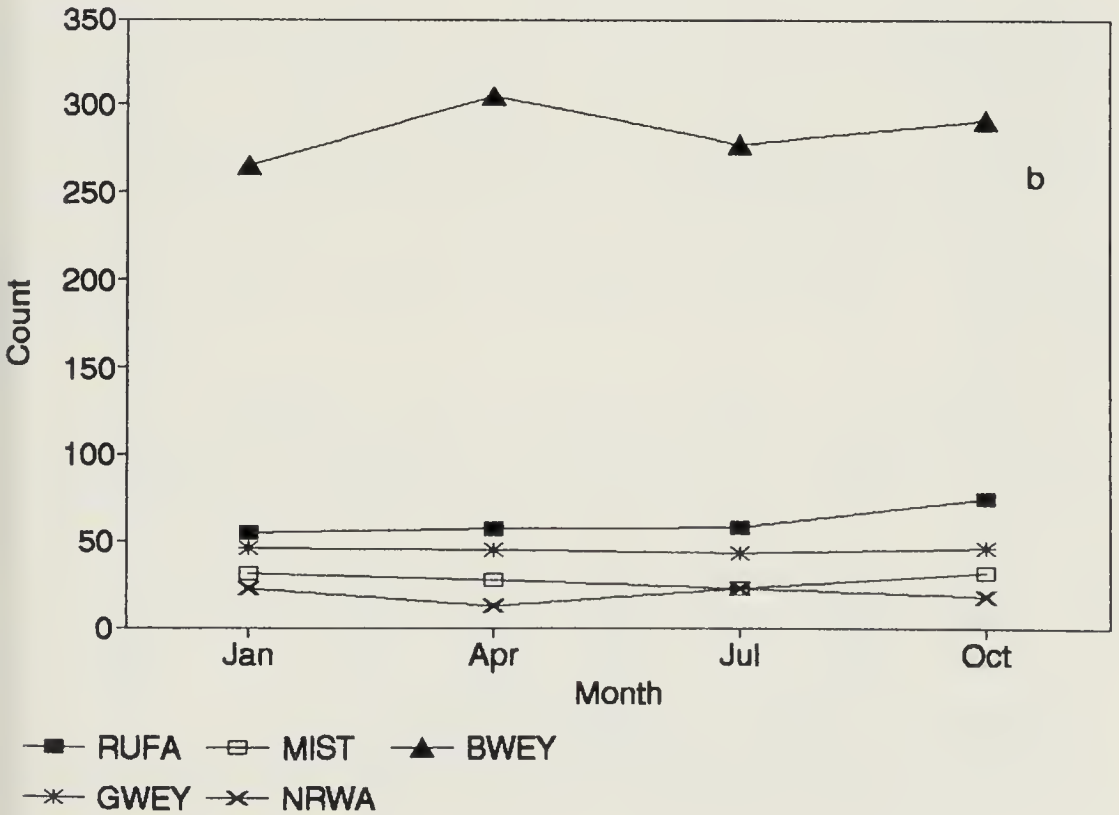
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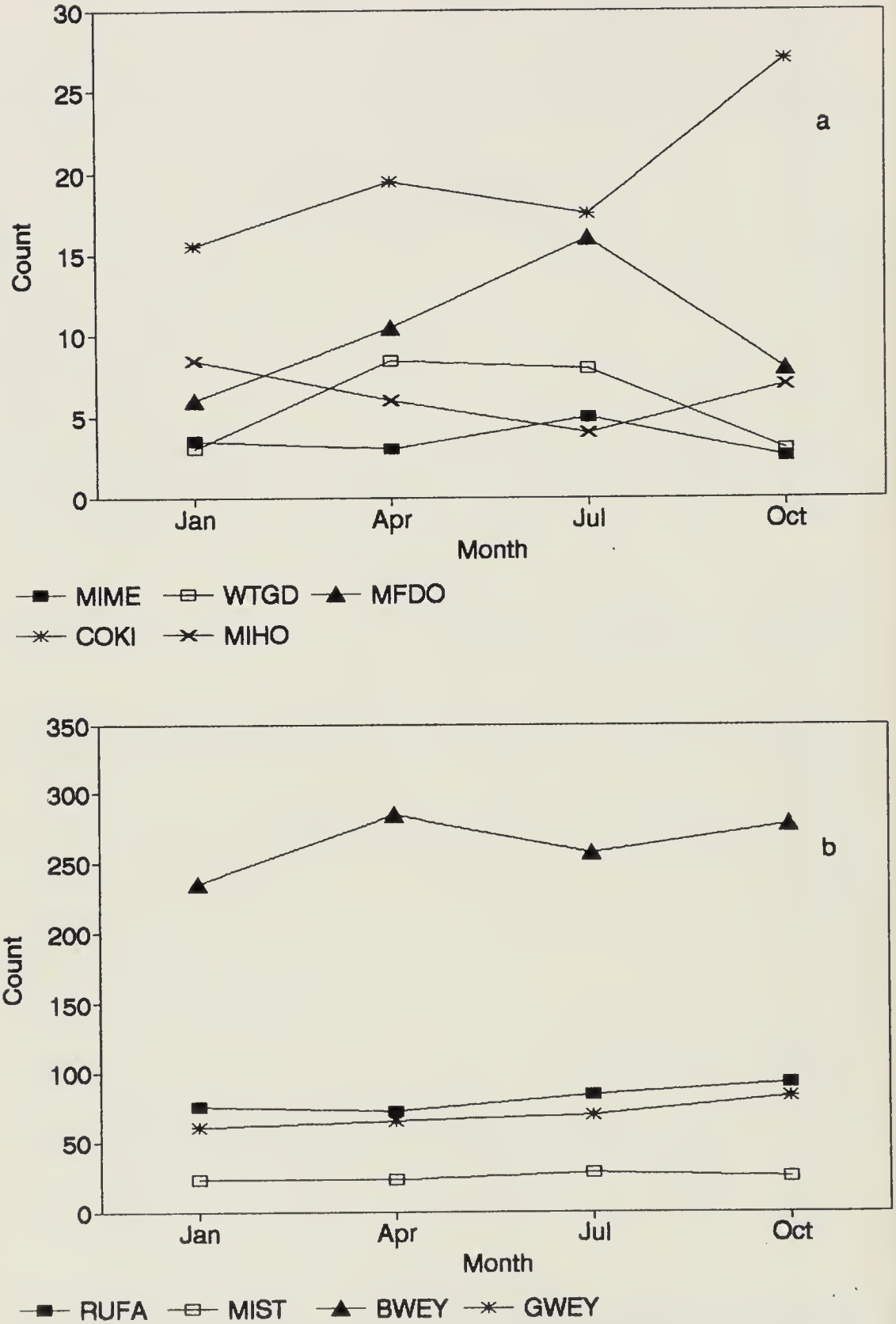

FIG. 3. Mean 1991–1992 population trends of land birds for limestone forest counts. See Fig. 2 for legend abbreviations.

TABLE 4
COEFFICIENTS OF VARIATION FOR 1991–1992 LIMESTONE FOREST AND ISLAND-WIDE SURVEYS, AND FOR 1993 REPLICATED (5 TIMES) VCP SURVEYS

Species	Limestone forest		Island-wide survey
	1991–1992	1993	1991–1992
Micronesian Megapode	43.2	27.2	82.8
Yellow Bittern	—	—	33.9
White-throated Ground Dove	57.0	64.4	52.9
Mariana Fruit Dove	50.3	35.2	62.7
Collared Kingfisher	15.1	22.9	15.0
Rufous Fantail	13.4	8.5	14.4
Nightingale Reed-warbler	—	—	29.9
Micronesian Starling	19.0	9.8	22.6
Micronesian Honeyeater	32.4	17.6	11.6
Bridled White-eye	13.4	4.3	18.5
Golden White-eye	18.5	5.0	12.9

Gut contents from two individuals collected on islands north of Saipan contained spiders, insects, seeds, and plant fragments (Stinson 1993a).

Yellow Bittern.—This species is typically categorized as a water bird (e.g. Engbring et al. 1986), and it indeed foraged in ponds, marshes, tidal flats, and shorelines. However, the Yellow Bittern also inhabited upland habitat mosaics in which grasslands were an important part. It was absent from the forests of the VCP transects (Table 2) but occurred uncommonly on the island-wide survey and showed weak October peaks each year (Fig. 2A). Direct counts were low at disturbed sites compared to those reported by Engbring et al. (1986) (Table 2), but my sample size was too limited for a valid comparison to be made or for population denities to be computed.

I recorded nesting in February (eggs) in a patch of elephant grass surrounded by tangantangan. Birds were seen in pairs and were observed flying hundreds of meters, thus suggesting that no all purpose territory existed. Observations of foraging were limited to two captures of lizards in upland habitat.

White-throated Ground Dove.—Although fairly common (but reported as rare by Jenkins and Aguon 1981), based on the frequency with which flying birds were seen, the species was otherwise visually inconspicuous and called infrequently. Such characteristics resulted in its being poorly censused. However, birds were usually encountered at close range (Table 1) and, therefore, densities computed (Table 3) were high relative to fruit doves.

Despite under-representation on censuses, three of four annual counts made at the two environmental scales peaked in April–July (Figs. 2A, 3A). Such a trend likely indicated an increase in breeding activity during those months (most census detections were of vocalizing birds). Indeed, Stinson (1993b) reported that all 14 nests in the Division of Fish and Wildlife (DFW) files were found between April and September. However, Jenkins (1983) provided evidence that the extinct Guam population could breed year round.

The cyclic nature of counts led to high coefficients of variation for census data compared to Saipan passerines, although even variation within a season was high (Table 4). Based on direct counts, the species appeared more frequent in native forest than in disturbed habitats and more frequent than found by Engbring et al. (1986) (Table 2). Computed densities followed similar trends (Table 3).

The White-throated Ground Dove on Saipan, Rota, and Aguiguan used a range of forest strata (Table 5), including the ground (N = 60). These observations contrast with those of Marshall (1949), Baker (1951), Jenkins (1983), and Engbring et al. (1986) who considered the species to be largely or entirely arboreal. On Saipan, it occurred in native forest, secondary forest, agriforest, tangantangan thickets, and habitat mosaics that included fields. In such habitats, it flew for at least 300 m above the canopy, suggesting that it did not defend all purpose territories.

Foraging observations included feeding on the ground on seeds and probing leaf litter (4), feeding on fruits of the native trees *Melanolepsis multiglandulosa* (1) and *Premna obtusifolia* (2), and inspecting papaya (*Carica papaya*) fruits (1). Marshall (1949), Jenkins (1983), and Villagomez (1987) list additional fruits eaten. Many members of the genus are forest understory herbivores (Beehler et al. 1986), but the White-throated Ground Dove appears to be more of a microhabitat generalist.

Mariana Fruit Dove.—All counts showed evidence of a population peak in April–July, although the trend was most pronounced in island-wide data (Figs. 2A, 3A). Data from 1983–84 and 1987 roadside call counts on Saipan (Villagomez 1987) showed a similar trend. As with the White-throated Ground Dove, these peaks appeared to represent increases in breeding activity rather than population cycles. Most census detections were of calling birds, and fruiting peaks by certain common native tree and vine species (e.g., *Ficus* spp., *Premna obtusifolia, Jasminum marianum*; unpubl. data) corresponded with these high counts. Wet season increases in breeding are known for New Guinea Fruit Doves (Frith et al. 1974). I recorded breeding in February (carrying nesting material), May (egg), and July (nestling), and Stinson (1993b) reported that 35 of 38 nests in DFW files were found between April and September.

TABLE 5
PERCENT USE OF FOREST ZONES BY NATIVE MARIANA ISLAND DOVES

Species	Forest zone			
	Top	Middle	Lower	Ground
White-throated Ground Dove	45.0 (27)[a]	20.0 (12)[a]	5.0 (3)[a]	30.0 (18)[a]
Mariana Fruit Dove	76.6 (49)[a]	21.9 (14)[a]	1.6 (1)[a]	0

[a] N.

Direct counts showed that the Mariana Fruit Dove was more common in limestone forest than in disturbed habitat, but uncommon compared to that reported by Engbring et al. (1986) (Table 2). However, because I encountered fruit doves at closer range than Engbring et al. (1986) (Table 1), density estimates for limestone forest were similar to those from 1982 (Table 3). Like the White-throated Ground Dove, the cyclic nature of counts produced high variation in seasonal census results. Variation was comparatively low within a season, although still higher than for passerines (Table 4).

The Mariana Fruit Dove appeared to focus activities (N = 64) in upper and mid-forest strata (Table 5). Otherwise, it occupied a range of habitats similar to that of the White-throated Ground Dove. Also, like the preceding species, it flew >100 m (often in pairs) above the canopy, suggesting that it did not defend all-purpose territories. I saw individuals feeding on fruits of the native *Ficus* spp. (9) and *Premna obtusifolia* (2) trees, the vine *Jasminum marianum* (1), and the introduced *Muntingia calabura* (1). Jenkins (1983) and Villagomez (1987) list additional fruits eaten by the Mariana Fruit Dove. Like many members of the genus (Beehler et al. 1986), this species is a canopy frugivore.

Collared Kingfisher.—Both limestone forest and island-wide surveys showed that three of four annual counts peaked in October (Figs. 2A, 3A). Seasonal variation in censuses was similar to that obtained for passerines, but lower than that for doves. Variation within was greater than that between seasons (Table 4), which illustrated the difficulty in censusing a species that regularly flew >300 m above the forest canopy. Densities computed (Table 3) are likely exaggerated because of the liklihood of overcount from flight calls made during these long flights. The Collared Kingfisher was encountered with similar frequency on limestone forest and disturbed habitat counts (Table 2), although because it was observed at greater distances in disturbed habitat (Table 1), its computed density was comparatively low. Engbring et al. (1986) found birds with similar frequency to that of this study (Table 2) but with lower computed density

(Table 3) because detection distances were lower in the present study (Table 1).

I detected breeding in January (recently fledged nest), May (nest), and June (nestlings, incubating). The Collared Kingfisher was present in every habitat, including shorelines, wetlands, savannah, disturbed sites, and limestone forest. In forest, I usually observed it flying above the canopy, at the forest edge, or perched in the top of canopy trees. However, it also entered the forest interior, where I mist netted individuals twice. It often occurred in pairs or groups of three to four birds, which probably were family groups.

I observed 15 feeding attempts by the Collared Kingfisher. Prey items included a millipede, grasshopper, unidentified insect, lizards (four confirmed, three apparent), Micronesian Honeyeater, Golden White-eye (attempt), and Bridled White-eye (capture, attempt, apparent capture). Marshall (1949) had previously listed insects, spiders, crabs, lizards, and mice as prey, and he also described frequent but unsuccessful attacks on Bridled White-eyes. Engbring et al. (1986) reported an instance of predation on a Rufous Fantail. The Collared Kingfisher is the only extant native predator on birds in the Marianas.

The importance of this species as a bird predator is reflected in observations of mobbing, scolding, and alarm calls directed against it by other species, including the Bridled White-eye (6), Golden White-eye (1), Rufous Fantail (1), and Micronesian Honeyeater (1). I also saw a Collared Kingfisher chase a Yellow Bittern (1) and fight with a Black Drongo (*Dicrurus macrocercus*) on Rota.

Island Swiftlet.—Because of its crepuscular nature, this species was poorly censused by the techniques employed, and census data are not reported. However, incidental dawn/dusk observations and data from the island-wide census demonstrated that, unlike most species, it was found unevenly about the island. Its distribution appeared correlated with the occurrence of suitable nest caves. Hence, it was common in mountainous areas around Takpochao, Capitol Hill, Navy Hill, As Teo, eastern Marpi, Laderan Hakmang, and Sabanan Nanasu but largely absent from western Marpi and flat lowlands throughout the island. I gathered no breeding or behavioral data on the Island Swiftlet.

Rufous Fantail.—Annual counts consistently peaked in October (Figs. 2B, 3B). Seasonal variation in counts was lower than that for doves, but variation within a season was still lower (Table 4), suggesting that populations or breeding status changed seasonally. The species was found with similar frequency in limestone forest and disturbed habitats (Table 2), although because birds were detected at greater distances in disturbed habitat (Table 1), computed densities there (Table 3) were relatively low.

Engbring et al. (1986) recorded the Rufous Fantail more frequently than did this study (Table 2), but their computed densities were far lower (Table 3) than in limestone forest, because my detection distances in forest were lower (Table 1).

Breeding was recorded for January (nest construction, eggs, fledglings, juveniles), February (eggs, juveniles), March (nest), April (nestlings), October (nest construction, eggs), and November (nestlings). Jenkins (1983) reported breeding in January–April, June, and November on Guam, and Marshall (1949) believed, based on gonad condition of specimens, that breeding occurred year round. Birds occurred commonly in a variety of wooded and thicket habitats, including beach strand and suburban habitats, but they were largely absent from swordgrass savannah.

Frequently observed food begging in small flocks of three to four birds indicated that these were family groups. Color banding further showed that groups remained at a single location. At such locations, males engaged in song duels with neighbors and responded aggressively to taped playback of songs. Hence, individuals appeared to defend all purpose territories.

Observations of interspecific aggression were restricted to one instance each of supplanting a Bridled White-eye at a perch and chasing a foraging Golden White-eye from near a fantail nest. More frequently, I saw birds following Golden (10) and Bridled white-eyes (10) to capture insects flushed by the foraging activities of these species.

Nightingale Reed-warbler.—I regularly recorded birds only on island-wide and disturbed site counts (Table 2). Birds detected on limestone forest surveys were almost all calling from outside the forest. Island-wide counts showed no clear seasonal trend (Fig. 2B). Previous studies at Marpi demonstrated a drop in territorial activity in the wet season by up to 24% (Craig 1992a). Indeed, my only breeding record was for February (fledgling). My inability to detect a similar island-wide trend by this loudly vocal species likely meant that the census data were inherently variable, although the local trend I found might not have been general.

In five years of observing on Saipan, I located Nightingale Reed-warblers in interior forest on only three occasions. These birds did not appear to be territory holders, because on subsequent visits to the same site they were absent. At the disturbed census sites (surveyed in March), I found individuals with lower frequency (Table 2) and density (Table 3) than did the more comprehensive Engbring et al. (1986) survey (made in May), although the species was generally widespread and common on the island. It occurred in all thicket-meadow mosaics, forest edge, reed marshes, and forest openings, but it was absent from beach strand and swordgrass savannah.

Because Nightingale Reed-warblers usually are concealed in thick vegetation, I recorded foraging rarely despite intensive study. Observations included eating insects (3), gleaning invertebrate from leaves (3) and a dead leaf (1), and probing a dead stub (1). Marshall (1949) reported insects, spiders, snails, and lizards as prey. Although the species was intraspecifically aggressive and defended all-purpose territories (Craig 1992a), I saw no interaction between it and other species.

Micronesian Starling.—This species showed little clear seasonal trend in censuses (Figs. 2B, 3B). Although seasonal variation in counts was low compared to doves, within-season variation was even lower (Table 4), suggesting a seasonal shift in populations or breeding status. Compared to limestone forest, it was encountered less frequently (Table 2) and observed to greater distances (Table 1) in disturbed habitats. Hence, computed densities (Table 3) were lower in disturbed habitats. It also was found more commonly in limestone forest than by Engbring et al. (1986) (Table 2).

Micronesian Starlings were usually seen in pairs, family groups (based on observations of adults attending food begging juveniles, mist netted juveniles with an aggressive adult nearby) or juvenile flocks (all birds in juvenal plumage). Larger flocks (5–11, not 50 as reported by Marshall 1949), made up mostly of birds in juvenal plumage were likely the product of several nestings by a single adult pair. As Jenkins (1983) reported for Guam, I observed single pairs nesting at the same location nearly year round. Banding showed that birds maintain a home range. The species used virtually all habitats from beach strand to interior forest and swordgrass savannah.

Jenkins (1983) listed a variety of fruits and seeds taken by the Micronesian Starling, and Marshall (1949) described it as omnivorous. I observed birds feeding on fruits of *Ficus* spp. (4), papaya (*Carica papaya*) (3), camachile (*Pithecellobium dulce*) (1) and an insect (1). Reichel and Glass (1990) reported that it preys on seabird eggs.

Micronesian Honeyeater.—No clear seasonal trend emerged in census data at either environmental scale (Figs. 2A, 3A). In limestone forest, between season variation was high compared to other passerines and to within-season variation (Table 4), suggesting that seasonal shifts occurred in populations or breeding status. Jenkins (1983) reported breeding on Guam year round, although he was uncertain if breeding peaks occurred. I recorded breeding in February (nest building) and May (courtship). It was uncommon in limestone forest compared to disturbed habitats, as well as to other passerines (Tables 2, 3). Engbring et al. (1986) found that the frequency (Table 2) and computed density of the Micronesian

Honeyeater was higher than I found for birds in limestone forest (Table 3).

The Micronesian Honeyeater was aggressively territorial against conspecifics, chased individuals and dispersed flocks of Golden White-eyes (4), and chased Rufous Fantails (2). I also saw a Micronesian Starling supplant a Micronesian Honeyeater at a perch.

At Capitol Hill, a color banded male had a territory of ca 0.7 ha. Two additional banded territorial males were observed to within 150 m from the banding site. However, repeated mist netting at one site yielded regular capture of unbanded birds (mostly females or juveniles, based on plumage and measurements) which indicated the existence of a population of nonterritorial birds. These floaters or nomadic birds may account for the seasonal variation in census data, because they may opportunistically follow ephemeral nectar sources as do certain of the Hawaiian Honeycreepers (Scott et al. 1986).

The species occupied a variety of habitats, including beach strand, mangroves, upland forest, suburban areas, and disturbed habitats. It was largely absent from swordgrass savannah, but particularly common in the vicinity of coconut (*Cocos nucifera*) groves where it fed on nectar. Foraging is discussed in detail by Craig and Beal (ms), and Table 6 lists 11 nectar sources that I recorded.

Bridled White-eye.—No clear pattern emerged in counts at either environmental scale, although January counts averaged lowest, probably because higher winds at this season reduced the detectability of this canopy species (Figs. 2B, 3B). Like most passerines, variation in counts was relatively low, and variation between seasons was greater than within a season (Table 4). Although even more individuals were encountered in disturbed habitats than in limestone forest (Table 2), birds detected were at greater distances so that population densities (Table 3) were lower in disturbed habitat. I recorded more Bridled White-eyes (Table 2), and densities computed were far greater than reported by Engbring et al. (1986) (Table 3), because I detected birds at closer range (Table 1).

Banded birds declined in frequency of occurrence, p, from the banding site to 300 m in an empirically fitted quadratic relationship ($r^2 = 0.99$):

$$p = 1.47x^2 - 1.21x + 53.82,$$

where x has values from one for the basal zone (0–50 m from the banding site) to six for the outermost zone (251–300 m). Based on this relationship, I solved Equation (3) for my Lincoln-Peterson (8754 bird/km^2) and Jolly-Seber (7770 birds/km^2) population estimates, which yielded densities of the same order of magnitude as those obtained through VCP censusing (Table 3).

TABLE 6

PLANT SPECIES FED UPON BY THREE SMALL FOREST PASSERINES

Plant species	Bridled White-eye				Golden White-eye				Micronesian Honeyeater			
	se[a]	fr	fl	ne	se	fr	fl	ne	se	fr	fl	ne
Vines:												
Momordica charantia	x	x			x	x						
Mikania scandens	?		x									
Passiflora foetida		x										
Operculina ventricosa				x								
Jasminum marianum		x	x									
Trees:												
Pisonia grandis			x	x				x				
Cynometra ramiflora			x	x								x
Premna obtusifolia		x	?	x		x						
Ficus spp.		x				x						
Melanolepsis multiglandulosa		x	?			x						
Erythrina variegata				x			x	x				x
Psychotria mariana				x		x		x				x
Morinda citrifolia				x				x				
Artocarpus spp.		x				x						
Aidia cochinchinensis							x	x				x
Pipturus argenteus		x										
Bikkia mariannensis												x
Hibiscus tiliaceus				x								x
Delonix regia												x
Lantana camara		x				x	x					x
Albizia lebbeck				x								x
Carica papaya		x				x						
Leucaena leucocephala			x									
Cocos nucifera												x
Muntingia calabura		x				x						
Herbs:												
Bidens pilosa	x											

[a] se = seed, fr = fruit, fl = flower, ne = nectar.

The Bridled White-eye was found in all habitats from beach strand to disturbed habitats, suburban areas, and forest. It was less common in swordgrass savannah. I recorded breeding in January (carrying nesting material), February (nestlings, carrying nesting material), August (eggs, carrying nesting material), and October (carrying food). Moreover, I observed food begging by juveniles year-round. Jenkins (1983) also reported that the Guam Bridled White-eye bred year-round. Although it is not territorial, banding demonstrated that birds remain in a home range, and

individuals could be attracted to playback of various flocking calls. Other than scolding Collared Kingfishers, interspecific social interactions involved only an observation of a Bridled White-eye following a foraging Rufous Fantail. No interspecific aggression initiated by Bridled White-eyes was noted. I recorded feeding on seeds, nectar, flowers, and fruit of 22 plant species (Table 6) in addition to invertebrates.

Golden White-eye.—No clear pattern emerged in counts at either environmental scale (Figs. 2B, 3B). Although as with other passerines, seasonal variation in censuses was relatively low, intraseasonal variation was still lower (Table 4). The Golden White-eye was decidedly more common in limestone forest than in disturbed habitats (Table 2, 3), although slightly less frequently encountered than by Engbring et al. (1986). Nevertheless, computed densities were greater in this study (Table 3) because I encountered birds at closer range (Table 1).

I recorded breeding in January (gathering nesting material, eggs, fledglings), February (eggs), March (eggs), May (recently fledged nest), June (eggs), July (copulation, carrying nesting material, eggs, nestlings), August (nest construction), and October (eggs). Moreover, I heard song and observed food begging year-round, except during the protracted dry season of 1993, when I heard no singing during June despite my almost daily presence in the field. This latter observation may help to explain Marshall's (1949) failure to detect any song in this species. Other than limited observations reported by Stinson and Stinson (1994), little other data on breeding exist.

Aggression involved chases and dispersing flocks of Bridled White-eyes (20) and Rufous Fantails (2). Golden White-eyes were territorial. Banded males defended territory boundaries against other males and responded, although not vigorously, to playback of recorded songs. Family groups of 3–4 (as demonstrated by food begging of juvenal plumaged birds) were typical. The Golden White-eye occurred in all wooded habitats, including strand forest and suburban areas, although it was generally absent from swordgrass savannah. Foraging is discussed by Craig and Beal (ms); I observed feeding upon invertebrates and the nectar, flowers, and fruit of 13 plant species (Table 6).

DISCUSSION

For seven of the nine forest bird species examined, census variation in limestone forest between seasons was greater than that within a season. The remaining two species possessed behavioral characteristics which made them particularly difficult to census. Hence, most or all forest species likely undergo seasonal shifts in either populations or conspicuousness (i.e., increased vocalizations related to breeding). In the case of

doves, strong shifts in vocalizing related to breeding activity are indicated. Many tropical forest passerines increase breeding activity during the wet season (Beehler et al. 1986), but only two species showed consistent peak counts at this time. These, the Collared Kingfisher and Rufous Fantail, are also the only Mariana Island forest species with widespread Indo-Pacific distributions. Other species showed divergence in seasonal counts between years, suggesting that no regular pattern in counts existed. Combined with evidence for year-round breeding for such species as the Micronesian Starling, Micronesian Honeyeater, Bridled White-eye, and Golden White-eye, seasonal variation in counts may, therefore, be caused by actual population shifts or differing peak breeding times related to resource availability. Storms, the vagaries of seasonal patterns, and attendant alteration in food supplies may drive such population or breeding shifts.

For many forest species, peak counts (7 of 9) and computed densities (8 of 9) were greater in native forest than in disturbed habitat. Therefore, native limestone forest, with its comparatively high diversity of tree species, its cooler, wetter microclimate, and variety of food sources, is likely to be superior habitat for most forest species. Only the Micronesian Honeyeater was noticeably more common outside native forest. Presumably, nectar is insufficiently abundant or consistently available to support high densities of this species in limestone forest. However, on nearby Aguiguan, which has forests similar to those on Saipan (Chandran et al. 1992), the Micronesian Honeyeater was common in native forest (Craig et al. 1992). Extensive stands of the introduced *Lantana camara,* are found adjacent to forest on Aguiguan but not Saipan. This shrub flowers year-round and is frequently visited by Micronesian Honeyeaters (Craig et al. 1992).

Censusing at two environmental scales uncovered few clear differences in seasonal trends. The principal difference uncovered was that the Micronesian Honeyeater was relatively uncommon in limestone forest but regular on island-wide counts. Otherwise, forest species showed numerous similarities in counts at both scales, thereby suggesting that a wide range of habitat was suitable for most.

Results of the Engbring et al. (1986) population survey of Saipan birds showed direct counts of roughly the same order of magnitude as those reported in this study. Major differences in counts probably result from this study's survey of primarily native forest, as opposed to all habitats in the 1982 survey. However, the much higher numbers of Mariana Fruit Doves and Rufous Fantails found by Engbring et al. (1986) are not easily accounted for and may indicate population declines in these species. Re-

cent surveys on Aguiguan also detected declines in counts of Mariana Fruit Doves compared to 1982 (Craig et al. 1992).

Although direct counts exhibited similarities, densities reported here are generally well above those computed by Engbring et al. (1986). Most of this difference may be attributed to the shorter distances at which I detected species. Recomputation of densities for my counts using the Engbring et al. (1986) distance estimates indeed yielded similar densities to those they obtained. Shorter detection distances were a consequence of my surveying only in dense, interior forest, whereas Engbring et al. (1986) censused in all habitats. Despite the large difference in results, I believe my density estimates are realistic. Independent density computations for the Bridled White-eye were of the same order of magnitude as those obtained through censusing. Moreover, Craig et al. (1992) pointed out that densities determined for such small passerines as the Golden White-eye translated to encountering one family group of four directly on the transect line once roughly every 100 m. Such a frequency is consistent with field experience for these species.

The densities reported here, particularly for the Rufous Fantail, Bridled White-eye, and Golden White-eye are among the highest ever reported for birds and are similar to those obtained for the most abundant of the Hawaiian Honeycreepers (Drepanidinae) (Scott et al. 1986). Indeed, personal observations of the Common Amakihi (*Hemignathus virens*) and Apapane (*Himatione sanguinea*) in the heart of their present range on Hawaii indicated that densities of Marianas small passerines were similar to those of these Hawaiian species. In temperate forests, in contrast, the density of the Ovenbird (*Seiurus aurocapillus*), the most abundant breeding species in two typical northeastern forest tracts, averaged 149.5–116.8 birds/km^2 (Magee 1989–1993a, 1989–1993b). These densities are about 1/15 that of the similarly territorial Golden White-eye and 1/44 that of the flocking Bridled White-eye. That such immense densities occur suggests that at least some forest birds in the Marianas exist at the maximum densities allowed by resources available in the habitat.

I cannot definitively attribute census variation to population fluctuations, because differences in breeding activity can also produce census variation. Further study is required to demonstrate that populations are at carrying capacity. However, existing at saturation densities is a characteristic of avian communities that is predicted to elicit interspecific competition, particularly between ecologically similar species (MacArthur 1972, Wiens 1977). Interspecific competition is most obviously manifested through aggression, and indeed the most ecologically similar of the small passerines, the two species of white-eyes (Craig 1989, Craig and Beal, unpubl. data) are those for which I observed the most aggression.

The larger Golden White-eye was clearly socially dominant over the Bridled White-eye, and much of the aggression observed involved chases of foraging Bridled White-eyes. Such behavior suggested that the contested resource was food. Based on observations on the four small passerines, the order of social dominance appeared to be Micronesian Honeyeater, Golden White-eye, Rufous Fantail, and Bridled White-eye. In contrast with temperate systems in which bird species can overlap widely in ecological space with little aggression because populations are rarely at saturation densities (Wiens 1977, Craig 1987), this study found aggression prevalent between species that were only generally similar in their ecology (Craig 1989, Craig and Beal, unpubl. data). The existence of populations at the carrying capacity of the habitat most likely accounts for this difference.

ACKNOWLEDGMENTS

My research benefitted from discussions on censusing proccdures with J. Engbring. It was funded in part by Pittman-Robertson Federal aid to wildlife.

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Wilson Bull., 108(2), 1996, pp. 268–279

NATURAL HISTORY AND CONSERVATION STATUS OF THE TAMARUGO CONEBILL IN NORTHERN CHILE

Cristián F. Estades[1]

Abstract.—I studied Tamarugo Conebill (*Conirostrum tamarugense*) populations at the Pampa del Tamarugal National Reserve in northern Chile between October 1993 and July 1994. The estimated population of conebills was 35,107 individuals in 10,787 ha of tamarugo forests. A strong relationship was found between forest foliage volume per hectare and breeding conebill density. The Tamarugo Conebill breeds in the tamarugal September–December and then probably migrates to the highlands of southern Perú. Although the species' breeding locality presently is protected, it faces some important threats including the pumping of the subterranean aquifers upon which the tamarugal vegetation depends, attempts to control the butterfly upon whose larvae the species forages, and human disturbance on the wintering grounds. *Received 15 May 1995, accepted 30 Nov. 1995.*

The western slope of the Andes, comprising the arid regions of northern Chile and southern Perú, is one of 57 areas of high avian endemism in South America (Bibby et al. 1992b). Among the birds of this region, the Tamarugo Conebill (*Conirostrum tamarugense*) is one of the rarest species, and has been known to science only since 1969 (Mayr and Vuilleumier 1983). The species was formally described by Johnson and Millie (1972) from six specimens collected at the Pampa del Tamarugal, northern Chile. Afterward, the few documented records of the species (see McFarlane and Loo 1974, McFarlane 1975, Tallman et al. 1978, and Schulenberg 1987) have provided little information about its natural history and general status. All records are of solitary individuals or small groups, generally in mixed flocks with the Cinereous Conebill (*C. cinereum*) (McFarlane 1975). Thus far, there have been no estimates of its population size, habitat requirements, or seasonal movements. Recently Estades and López-Calleja (in press) have reported the nesting of the species at the Pampa del Tamarugal. The conservation status of the Tamarugo Conebill is uncertain, and the Chilean Forest Service (CONAF) considers it "insufficiently known" (Glade 1988). More recently Rottmann and López-Calleja (1992) considered the Tamarugo Conebill as "vulnerable," while Collar et al. (1992) also categorized the species as "insufficiently known" in the list of threatened birds of the Americas.

The present paper reports on an assessment of the conservation status of the Tamarugo Conebill (*C. tamarugense*) in northern Chile. The objectives of the study were to obtain estimates of the species' population

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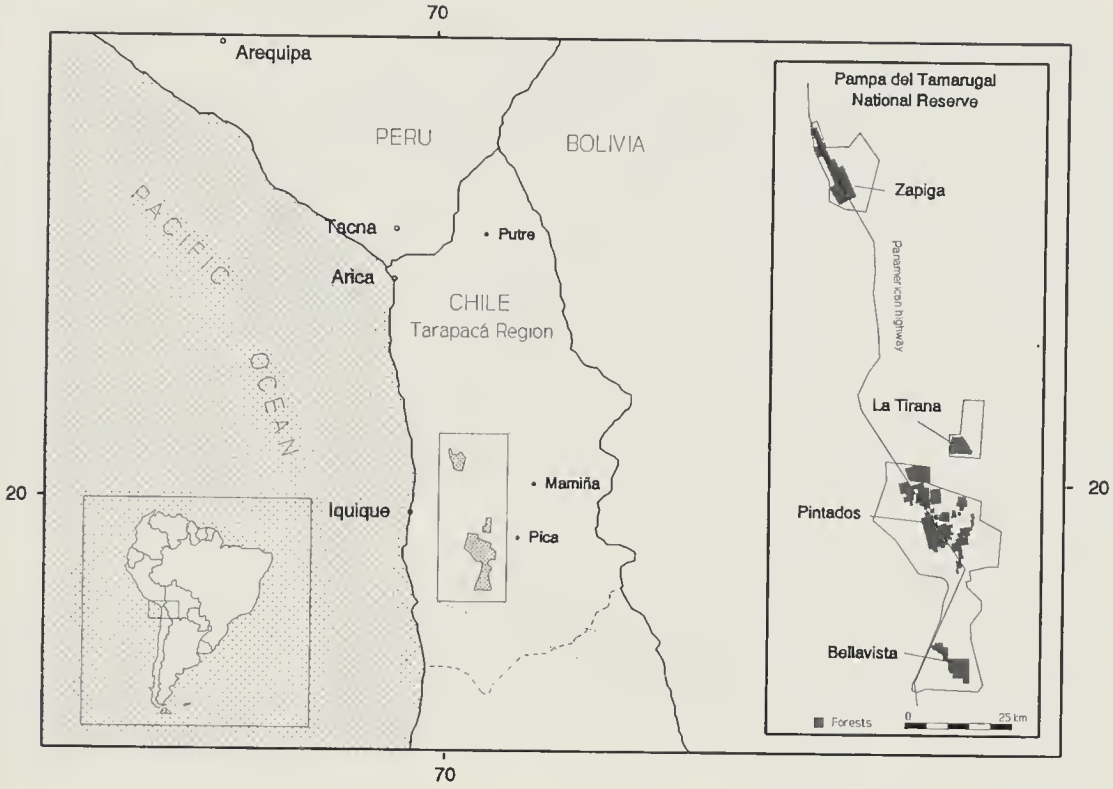

FIG. 1. Geographical location of the study area.

size, describe its habitat requirements, assess its seasonal movements, and determine principal threats to its survival.

STUDY AREA AND METHODS

I studied conebills at the Pampa del Tamarugal National Reserve (20°24′S, 69°44′W) in the Tarapacá Region, northern Chile (Fig. 1). This area, at an elevation of 1000 m, has an extreme dry climate with a mean annual rainfall of 0.3 mm (di Castri and Hajek 1976). Annual temperatures range between an absolute minimum of −12°C and a maximum of 35°C. Relative humidity undergoes wide daily fluctuations (3–8% during the day to 80–100% during the night in October; Sudzuki 1985). The Pampa del Tamarugal is a vast salt flat over subterranean aquifers. It is dominated by savannas of tamarugo (*Prosopis tamarugo*), a highly drought-resistant tree. Shrub and herbaceous layers are almost nonexistent, with only scattered individuals of *Atriplex atacamensis, Tessaria absinthioides, Caesalpinia aphylla,* and the extreme halophyte *Distichlis spicata* (Gajardo 1994). During the last four centuries, the Pampa del Tamarugal was intensively exploited for the production of firewood and charcoal, mainly to support the mining industry. This cutting drastically reduced the extent of the tamarugo forest, leaving few remnants of forest, mainly low density stands of little economic interest. In the 1930s, a reforestation program was started, which by the 1970s had generated 14,600 ha of tamarugo plantations (Aguirre and Wrann 1985). In addition, approximately 1900 ha of algarrobo (*Prosopis alba*) plantations were established at the Reserve. In 1983 the administration of the plantations passed to the Chilean Forest Service which created the 109,842-ha Pampa del Tamarugal National Reserve (Fig. 1). Since its creation, the reserve has been used for the production of forage for sheep which feed on

tamarugo pods, for the production of firewood and charcoal, and, occasionally, for the production of lumber.

I visited the Pampa del Tamarugal three times between October 1993 and July 1994. The first visit (25 Oct–2 Nov) was during the austral spring, the second (14–21 March) during late summer, and the third (19–26 July) during mid-winter. The reserve is divided into four major areas: Pintados, Bellavista, La Tirana, and Zapiga (Fig. 1). Due to time constraints, only the first three plots were assessed. These areas were selected for the following reasons: Pintados is the largest stand and holds the oldest tamarugo plantations, Bellavista is at the southern limit of the Reserve and might correspond to the southern limit of the Tamarugo Conebill's range, and the La Tirana plot holds the last natural tamarugo stands.

In order to estimate population densities 18 line transects were established at Pintados and six at Bellavista in the spring of 1993. Because no birds were found at La Tirana during the surveys, no transects were established and density was considered to be zero. Three of the transects at Pintados were located in a 60-ha managed stand. The trees of the latter stand had been pruned in 1991 for the production of timber and charcoal. As a result of this management, these trees lacked almost the entire lower half of their foliage. Additionally, four transects were surveyed at an algarrobo plantation at Pintados.

The transects used were of the "fixed belt" type (Bibby et al. 1992a). In each transect, all the birds seen or heard between two rows of trees were counted. Thus the width of the belt was two times the distance between tree rows. Because this distance was different between years of planting (10, 13.5 or 15 m) the length of the transects varied from 300 to 200 m, in order to equalize the surveyed areas. Preliminary observations carried out in the afternoon (i.e., after 13:00 h) consistently gave lower densities than observations in the morning. Therefore, all surveys were made between 7:00 and 12:00 h. Transects were surveyed 3.1 times, on average, during the first visit.

During March and July 1994, four of the transects at Pintados were surveyed a total of eight times per visit in order to compare densities between seasons. The other transects were not formally assessed.

Habitat along transects was characterized in terms of foliage volume per ha. The estimation of each tree's volume (m^3) was based on the formula volume = $(0.5 \text{ diameter})^2 \times \text{pi} \times \frac{2}{3}$ height. The estimated dimensions of the trees were total height, crown diameter, and presence or absence of the lower third of the foliage. To convert the results to volume per ha, the number of trees in the transect was recorded.

To describe the patterns of microhabitat use by foraging conebills, I divided trees visually into six sections. The parts of the tree that contained the leaves and flowers were separated from those that consisted of leafless branches, and the tree was divided into three horizontal layers. All observed birds were assigned to the section in which they were first observed. Individuals were captured in mist nets and banded to study the species' migratory movements. Finally, non-systematic observations were made to expand knowledge of the species' general natural history, both in the reserve and in adjacent localities. Mean densities were compared among seasons using one-way ANOVA. The effect of tamarugo pruning on bird density was assessed using a *t*-test.

RESULTS

Population size.—Densities derived from transects were calculated separatedly for the different types of tamarugo forests surveyed during spring 1993. During this period, many conebills were observed throughout the tamarugo plantations but at varying local densities (Table 1). No individuals were found at La Tirana. The total estimated conebill popu-

TABLE 1

DENSITIES (IND/HA) AND POPULATION SIZES OF TAMARUGO CONEBILL IN PAMPA DEL TAMARUGAL NATIONAL RESERVE, NORTHERN CHILE, DURING OCTOBER 1993

Stand	Stand age	Stand area (ha)	Conebill density mean (SD)	Total population
Pintados	46	964	9.27 (2.85)	8940
Pintados	27	2881	4.84 (3.23)	13,947
Pintados	21	4833	2.38 (3.39)	11,517
Bellavista	21	2109	0.33 (1.49)	703
All stands	—	10,787	3.25 (0.68[a])	35,107[b]

[a] Weighted mean's standard deviation (Cochran 1980).
[b] 95% confidence interval: 18,970–51,244; 11.3 degrees of freedom.

lation was 35,107 individuals. At Pintados, significant differences were found between conebill densities in different seasons (Fig. 2). Densities declined ($F = 74.37$, df = 2, $P = 0.000$) over time from a high of 8.3 ind/ha in October 1993 (breeding season) to almost no birds at all in July 1994 (nonbreeding season).

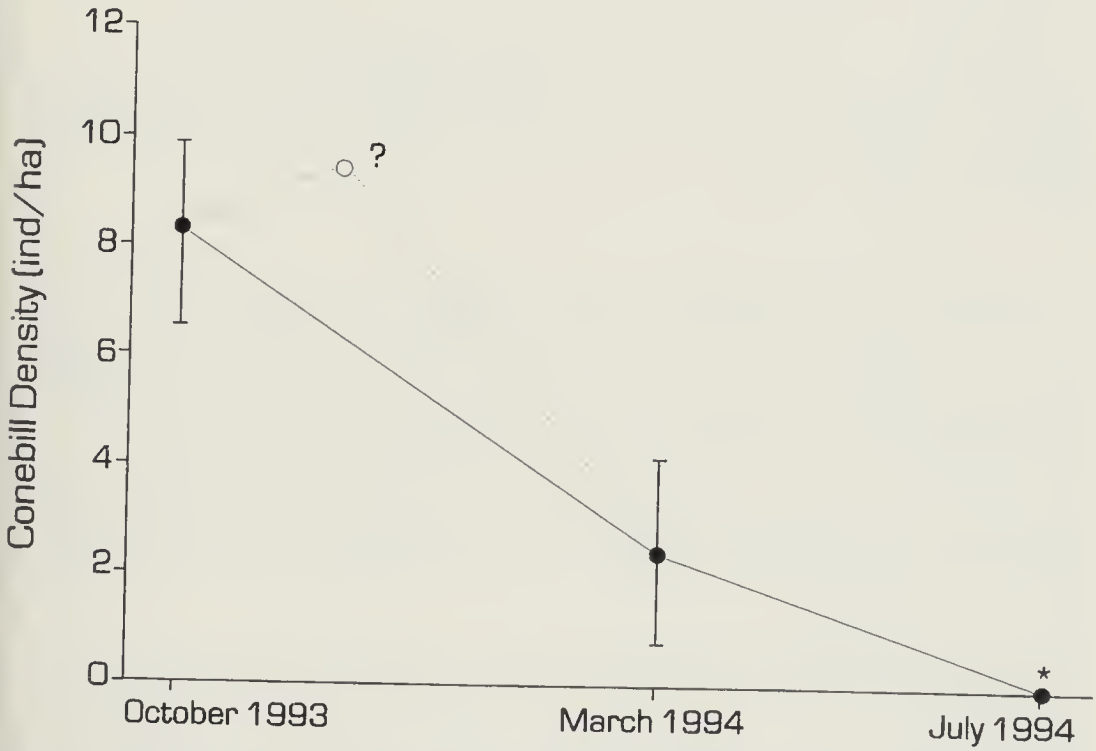

FIG. 2. Mean conebill densities (±SD) on four transects in a 46-year-old forest stand at Pintados for three periods. The empty circle with the interrogative symbol represents the possibility that the population had increased in November–December due to the addition of first-year birds following the breeding season. The asterisk indicates individuals were observed in the area, but none was recorded on the transects.

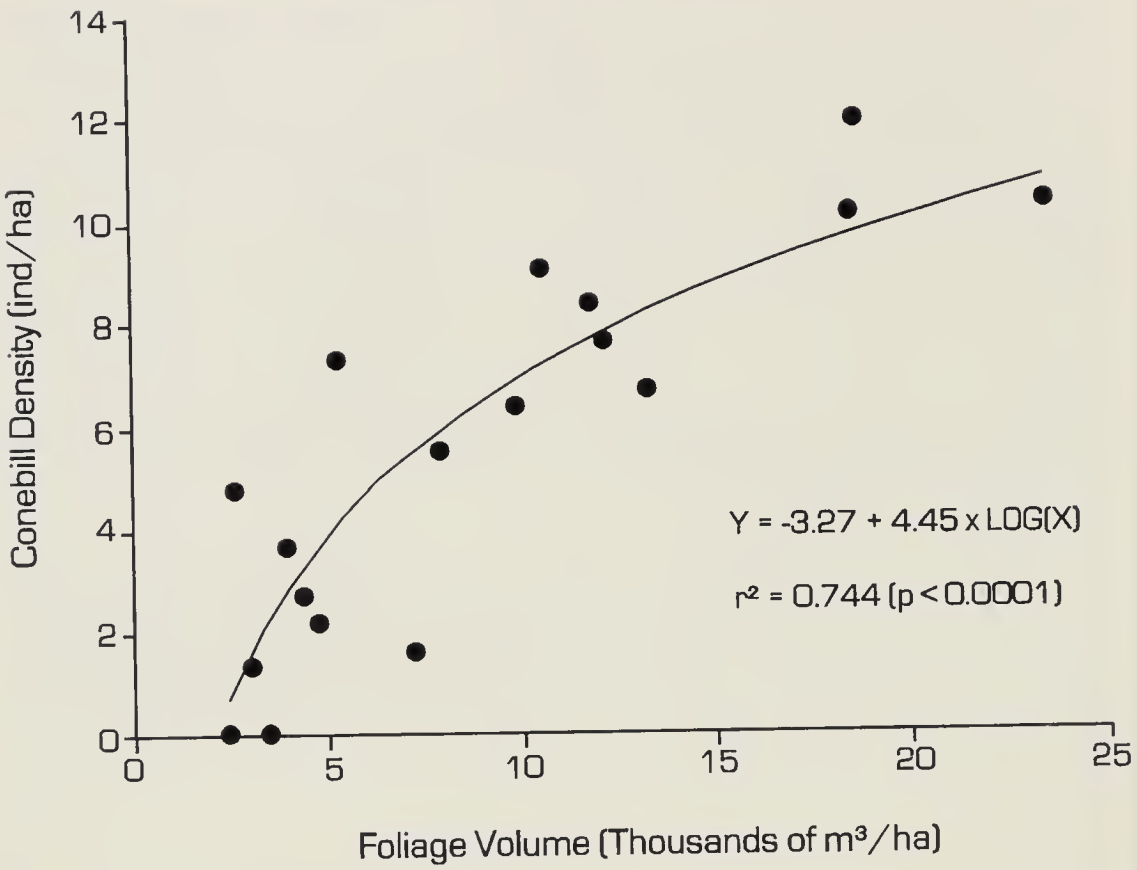

FIG. 3. Relationship between tamarugo foliage volume per ha and conebill density during October (breeding season) 1993 at Pintados. Points represent the mean conebill density on each transect.

Habitat use.—A significant relationship was observed between forest maturity and density of breeding conebills (October 1993). At Pintados, a high percentage of the variance ($r^2 = 0.744$; N = 18; $P < 0.0001$) of conebill density is explained by the total foliage volume (Fig. 3). Surveys of algarrobo plantations show that the Tamarugo Conebill does not use this forest type; on the four transects, no individuals were seen (October 1993). During the breeding season, the managed stand at Pintados held a significatively lower density of conebills than the unmanaged stands (*t*-test, $P = 0.0000$).

The species was found wintering (July 1994) at the localities of Pica and Mamiña (see Fig. 1). At the first site, a few individuals were observed foraging with *C. cinereum* in *Citrus* plantations. The same situation was found at Mamiña, where conebills were foraging in mixed flocks in riparian scrubs of *Baccharis petiolata* and *Tessaria absinthioides*.

Microhabitat use.—During the breeding season, the Tamarugo Conebill showed a marked tendency to use the outer and upper parts of tamarugo

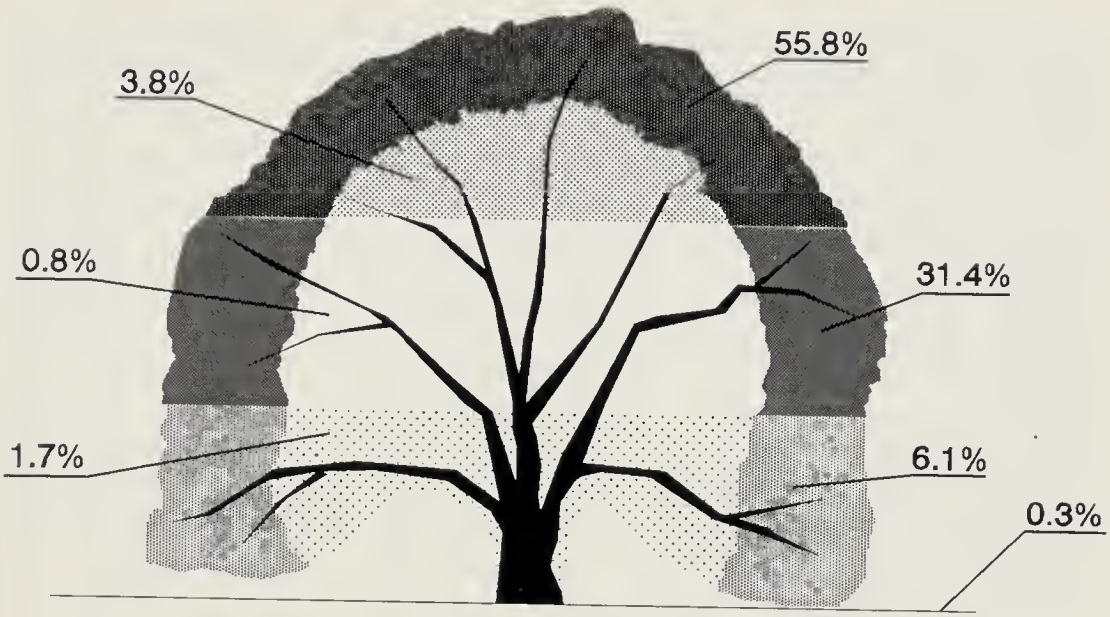

FIG. 4. Percent of sightings of conebills in each tamarugo microhabitat zone.

trees (Fig. 4). The species was observed foraging mainly on Lepidoptera larvae, specifically on the species *Leptotes trigemmatus* Butler (Lycaenidae) which feeds on tamarugo leaves, buds, and flowers (Cogollor et al. 1982). Conebills preferentially selected the descending terminal branches of the trees for nesting (Estades and López-Calleja, in press). In the oldest forests, breeding pairs held territories that included only a few trees around the nest tree. During the nonbreeding season, the species did not show a clear pattern of microhabitat use at Pampa del Tamarugal. At the other sites surveyed, the species foraged mainly inside the scrub.

Because conebills principally used the upper half of tamarugo trees for foraging, I thought that the removal of the lower half of the crown (as a result of the pruning of the trees in the managed area) might have little impact on the birds, but their density was lower in the managed stand. The hypothesis that pruning created microclimatic changes that may have affected the habitat suitability of the trees was tested. In July 1994 air temperatures were measured at ground level and at 1.5 m and at 4.5 m at the center of 15 pruned and 15 non-pruned trees and then averaged. Data were collected at 7:00 and 12:00 and repeated over two days. No significant differences were found between pruned and non-pruned trees at 7:00 h (t-test, $P = 0.635$). At 12:00 h, mean temperature was significantly lower at the pruned plot (t-test, $P = 0.009$), probably due to the convective cooling of wind.

Breeding.—The nesting of *C. tamarugense* was first recorded at Pintados in October 1993, austral spring (Estades and López-Calleja, in

press). These authors found several active nests and presented evidence that the species has been breeding at the Pampa del Tamarugal for many years.

Breeding success was not evaluated. However, during March 1994 (late summer), conebills at the reserve were observed flying in small flocks composed of approximately 60% adults (individuals with the rufous superciliary line, throat, upper breast, and undertail coverts) and 40% immatures. The only juvenile conebill captured was slightly smaller than the adults and showed a dirty grayish color instead of the characteristic rufous pattern.

During July 1994 (winter), very few individuals were observed at the reserve (0–6/day). It was not possible to determine their age since all were seen from a distance. However, many of the conebills observed at the Mamiña oasis lacked the rufous adult color.

DISCUSSION

Habitat and distribution.—Even though *C. tamarugense* is not restricted to tamarugo forests (McFarlane 1975, Tallman et al. 1978, this report and several personal communications), the species depends on this type of vegetation for breeding. Moreover, given the high concentration of individuals and reproductive activity (Estades and López-Calleja, in press) and the absence of significant tamarugo forests outside the reserve, it seems possible that most, if not all, of the species' population breeds in this area. Maturity of the forest seems to be an important factor in determining the habitat suitability for conebills. The strong relationship between foliage volume per hectare and the density of breeding conebills parallels patterns described by Mills et al. (1991). Considering that the number of flowers and the density of larvae in these flowers at Pintados are correlated positively with tamarugo foliage volume (López-Calleja and Estades, unpubl. data), the relationship between conebill density and foliage volume (Fig. 3) suggests that, above a certain foliage volume, conebill density could be limited by territoriality instead of availability of food. Below approximately 2000 m^3 of foliage per ha, the tamarugo forest is not a suitable habitat for the Tamarugo Conebill (Fig. 3). This hypothesis could explain the absence of the species at La Tirana. Even though foliage density was not formally assessed at this site, it was clearly below 2000 m^3, as trees are separated by 30 m or more in this area.

Low density of conebills at Bellavista could be explained by the scarcity of *Leptotes* larvae feeding on tamarugo flowers there (López-Calleja and Estades, unpubl. data). This situation could be due to the high degree of isolation of the plot which may reduce immigration of these butterflies.

The high proportion of time spent by the species at the top of trees

(see Fig. 4), might be mainly due to the concentration of flowers and *Leptotes* larvae there, rather than a territorial behavior. In fact, breeding conebills, instead of singing from high branches, call constantly while looking for food, as stated by Fjeldså and Krabbe (1990).

Johnson and Millie (1972) and Tallman et al. (1978) suggested that the Tamarugo Conebill could be a high-altitude species that breeds during the summer (highlands breeding season), then in winter moves into lowlands of Tarapacá until the spring (late lowlands breeding season). Our present study does not support this hypothesis, indicating instead that breeding occurs at Pampa del Tamarugal between September and December during the tamarugo flowering and the outbreak of *Leptotes trigemmatus* larvae. Individuals may then move upwards (to 2500–3500 m) and to the north, following a chain of small, mid-elevation, vegetated valleys. Possibly a small group could also migrate to the north from or through Zapiga to the lowlands of Arica, where the species has been observed (McFarlane 1975) (Fig. 5). Given the results of this study, isolated individuals or small flocks of the species seen in lowlands near Arica during the breeding season (Sept.–Nov.; McFarlane 1975, Sallaberry pers. comm.) are probably wandering, nonbreeding birds. This uncommon pattern of migration would enable the species to use an important food resource almost exclusively during its breeding period (no other bird species was observed foraging on *Leptotes* larvae at the Pampa del Tamarugal) and thereafter to share seasonally rich food resources with the species of the highlands of northern Chile and southern Perú during their breeding season (Jan.–March).

It is possible that some conebills could remain near the Pampa del Tamarugal during the entire year, since in May–June the tamarugos have a second flowering period ("devareo"). However, the extent and intensity of this phenomenon seems to be insufficient to support a large conebill population.

Conservation status.—The relationship observed between the vegetation and Tamarugo Conebill density suggests that, in the year of the species' discovery (1969) the oldest of the reforested forests (which then had a mean age of 23 years) were just beginning to provide a suitable habitat for the species, allowing its populations to reach a level that permitted detection by ornithologists. This hypothesis implies that the present population of the species is derived from a small number of individuals that survived a major population decrease during the period of deforestation at Pampa del Tamarugal.

My estimates for the total population of *C. tamarugense* at the study area are larger than any of the general estimates for minimum viable populations (see Shaffer 1987). In addition, assuming that the relationship

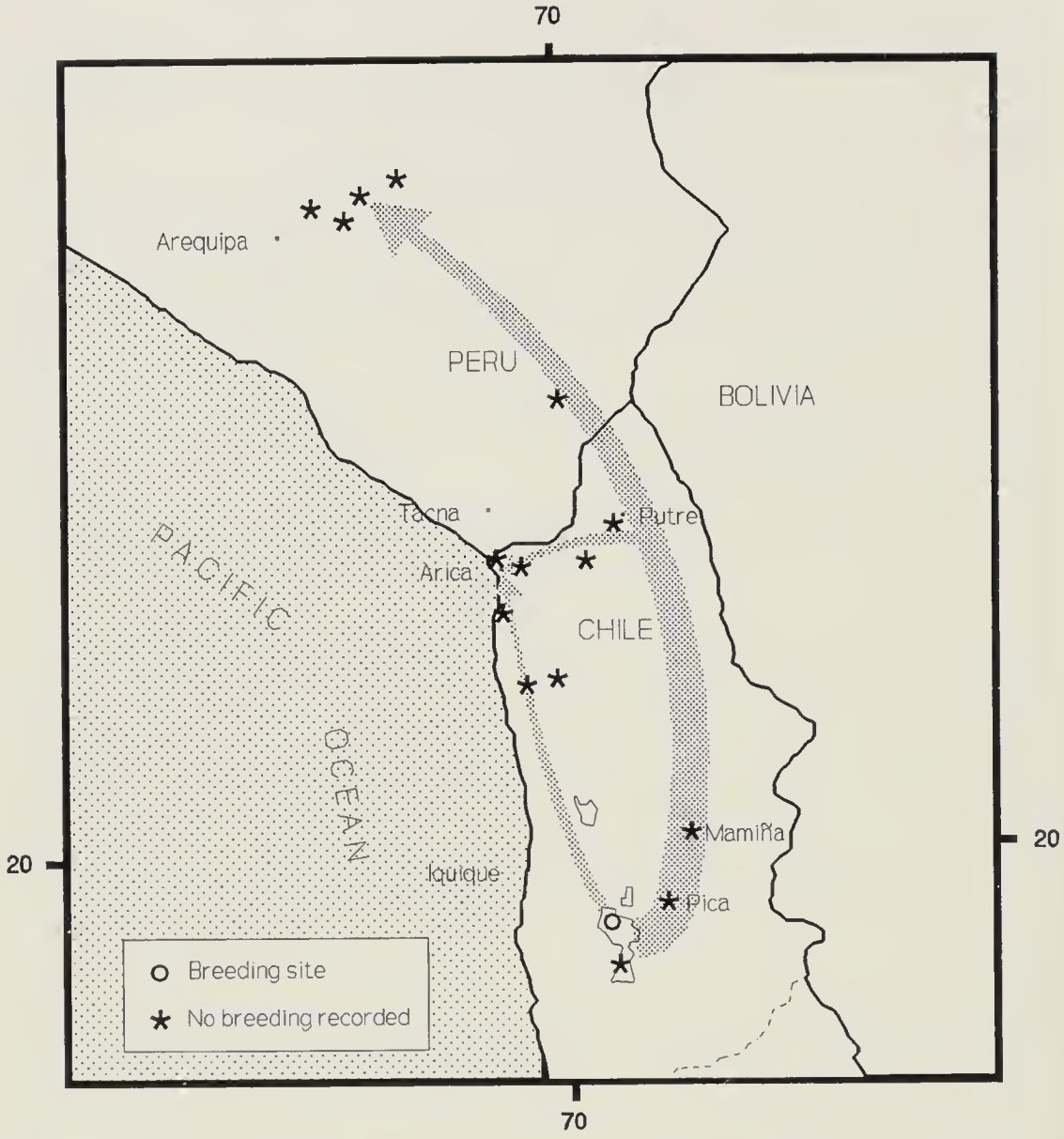

FIG. 5. Known localities (symbols) and hypothetical migratory movements (arrows) of *C. tamarugense*.

between vegetation and conebill density will not change during future years, the total population of the species should increase with the forest volume as younger plantations mature. However, even if Tamarugo Conebill populations are increasing and viable, there are at least three major threats that could reduce the species' short-term survival probability. (1) Presently the tamarugo is still managed mainly for production of sheep forage (pods) and for production of timber and charcoal, and pruning of trees reduces habitat suitability for conebills. However, management techniques could be modified in order to reduce the negative impact on the

birds. The threat of forage production is quite different, because management attempts to control populations of *Leptotes trigemmatus,* which feed on flowers and drastically reduce the yield of pods. Initially it was intended to control the species by using chemicals (Cogollor et al. 1982). At present, the Chilean Forest Service is studying the use of parasitoid microhymenoptera as an alternative way of control. The success of such a control program could, without doubt, be extremely harmful for conebill populations. (2) Since the mean annual rainfall in the area is 0.3 mm, the only water available for the tamarugos are the subterranean aquifers that are found beneath the Pampa del Tamarugal. At present, these waters are pumped at a rate of 700 lts/sec (CONAF rangers, pers. comm.) in order to supply the requirements of the city of Iquique (see Fig. 1). The ecological consequences of this water removal are not known. It is not clear whether these aquifers are recharged by rainfall in the mountains, or if they are "fossil" waters. In the last few years, there has been an increasing number of dead trees observed at several sites in the reserve. However, this phenomenon has been related to an excessive salt accumulation within the xylem vessels rather than to water deficit (Donoso et al. 1989). (3) Almost all localities where *C. tamarugense* has been observed, out of the Pampa del Tamarugal National Reserve, seem to lack of any type of legal protection. During the non-breeding season, the Tamarugo Conebill has been reported foraging in sites dominated by tree species such as *Polylepis,* shrubs such as *Gynoxys* in Perú (Tallman et al. 1978), and scrub (*Tessaria, Baccharis*), trees (*Schinus*) and cultivated species (*Citrus*) in Chile (McFarlane and Loo 1974, McFarlane 1975, this study). Even though there are no direct threats to conebill populations at the species' wintering localities, all these areas are characterized by extreme aridity, and there is increasing human disturbance (e.g., *Polylepis* cutting). The security of the species' wintering grounds is, therefore, uncertain (Collar et al. 1992).

I suggest the following: (1) To give the species the IUCN conservation status of "Vulnerable," as suggested by Rottmann and López-Calleja (1992). Further research and population monitoring should continue to clarify its status. (2) To stop or limit the control of *Leptotes trigemmatus.* An economic assessment would be necessary in order to estimate the cost of not controlling this insect. (3) To study the short- and long-term effects of tamarugo management strategies on conebill populations in order to design management techniques that best benefit all tamarugo users. (4) To study the effects of water pumping on the survival of Tamarugo Conebills.

ACKNOWLEDGMENTS

I thank M. V. López-Calleja, H. J. Hernández, and P. B. Aguirre for their valuable field assistance. The Chilean Forest Service (Conaf) gave permission to work at the Pampa del Tamarugal National Reserve and provided some assistance. G. H. Rosenberg kindly shared with me his field observations. I thank J. Jiménez for his review of an earlier draft of the manuscript. I also thank J. M. Bates, J. P. O'Neill, C. R. Blem, and S. A. Temple for their helpful comments on this paper. This study was supported by the Pan American section of BirdLife International and the U.S. Fish and Wildlife Service.

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AVIAN ABUNDANCE IN RIPARIAN ZONES OF THREE FOREST TYPES IN THE CASCADE MOUNTAINS, OREGON

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ABSTRACT.—We surveyed bird populations along headwater streams of old-growth, mature, and young coniferous forests of the Oregon Cascade Mountains during summer and winter. Brown Creepers (*Certhia americana*), Chestnut-backed Chickadees (*Parus rufescens*), Golden-crowned Kinglets (*Regulus satrapa*), Evening Grosbeaks (*Hesperiphona vespertinus*), and Winter Wrens (*Troglodytes troglodytes*) were common in all stand types. During the summer, abundances of Brown Creepers, Hammond's Flycatchers (*Empidonax hammondii*), Hermit/Townsend's warblers (*Dendroica occidentalis*), and Chestnut-backed Chickadees were significantly higher in old-growth and mature forests compared to young forests. Species richness and densities generally were not significantly different among the stand types during winter. However, numbers of Chestnut-backed Chickadees, Evening Grosbeaks, Golden-crowned Kinglets, Hairy Woodpeckers (*Picoides villosus*), and Winter Wrens were much higher in the winter than in summer. Swainson's Thrushes (*Catharus ustulatus*) and Rufous Hummingbirds (*Selasphorus rufus*) were more abundant in riparian areas in this study compared to other studies in upland forests and may be riparian associates along these headwater streams. *Received 4 Oct 1994, accepted 20 Oct. 1995.*

Complexity of streamside vegetation associated with the aquatic and terrestrial interface creates unique habitats which are generally high in wildlife diversity and abundance (Thomas et al. 1979, Bull and Skovlin 1982). This is especially true in arid land environments or along large streams and rivers where riparian vegetation is markedly different from upland vegetation (Johnson and Jones 1977). However, vegetative communities along small mountain streams within western coniferous forests are less distinct from upland areas because conifers dominate and suppress the deciduous components of the riparian community (Swanson et al. 1982). The importance of these mountain streams as habitat for birds has been largely overlooked to date, especially in the dense forest lands of the western Cascade Mountains.

The rapid liquidation of old-growth forests and their recognition as unique wildlife habitat has made old-growth management a major forestry-wildlife issue in the Pacific Northwest (Meslow et al. 1981). Initially, the old-growth issue focused on the Northern Spotted Owl (*Strix*

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occidentalis), but other studies have indicated that many more species of wildlife may find optimum habitat in old-growth forests (Meslow 1978; Thomas 1979; Verner and Boss 1980; Anthony et al. 1982; Mannan 1980, 1982; Manuwal 1991).

In this study, we compared abundance of birds in small riparian zones among old-growth, mature, and young-aged forests. Specifically, species richness and density of the avian communities were compared among stand types and between summer and winter seasons.

STUDY AREAS AND METHODS

The study was conducted in the western hemlock (*Tsuga heterophylla*) zone of the Oregon Cascade Range on the Blue River and McKenzie River Ranger Districts of Willamette National Forest, Lane County, Oregon. Study areas were located along riparian zones of second and third-order streams within old-growth (400–450 yrs), mature (130–200 yrs), and young (25–35 yrs) forest stands. Five study areas were selected in both old-growth and mature stands and two in young stands. Old-growth stands were natural, unharvested forests, and mature stands were relatively even-aged and originated from an extensive wildfire during the 1850s. Young stands originated from clear-cut forest practices. Study areas ranged in mean elevation from 490–975 m and varied in slope and aspect. Annual rainfall is approximately 180 cm.

Douglas-fir (*Pseudotsuga menziesii*) dominated the forest community in all successional stages. Western hemlock and western red cedar (*Thuja plicata*) contributed to the old-growth canopy. Western red alder (*Alnus rubra*) was a conspicuous component of the young stands and was co-dominant with big-leaf maple (*Acer macrophyllum*) and willow (*Salix* spp.). The shrub layer included salmonberry (*Rubus spectabilis*), red huckleberry (*Vaccinium parvifolium*), vine maple (*Acer circinatum*), salal (*Gaultheria shallon*), Pacific rhododendron (*Rhododendron macrophyllum*), dwarf Oregon grape (*Berberis nervosa*), western swordfern (*Polystichum munitum*), and common bracken fern (*Pteridium aquilinum*). The young-aged stands had the lowest shrub cover because of the dense overstory of young Douglas-fir and western red cedar; however, early seral plants such as willow and snowbrush ceanothus (*Ceanothus velutinus*) were common.

We established five plots at 200-m intervals along the riparian zone in each of the 12 study areas. Inclusion of more than five plots was not possible because of difficulty of locating homogeneous habitats that were more than 1 km long. Stream noise was minimal, because the streams were small (1–3 m wide). Birds were surveyed using the variable circular plot method (Reynolds et al. 1980). Each plot was sampled once per week for 10 min during the period of dawn to 10:00 h. Each bird seen or heard during the sample period was identified, and the distance from their location to the plot center was estimated and verified with range finders. Surveys were repeated five to seven times during summer (May–June) and six times during winter (Jan–Feb). The third and fourth authors conducted the surveys and alternated visits to a stand to minimize observer bias.

Estimates of bird density were determined by the method first described by Emlen (1971), and later modified by Ramsey and Scott (1981), to distance sampling of birds. At least 15 detections per species over all stands were required for the algorithm to estimate detection distances and generate density estimates. Densities were not estimated for species with <15 detections.

Differences in densities between seral stages were tested using analysis of variance with Duncan's multiple range test for mean separation (Steel and Torrie 1980:187). All statistical

TABLE 1

COMMON NAMES, SCIENTIFIC NAMES, AND ABBREVIATIONS FOR BIRD SPECIES OBSERVED DURING THE STUDY

Common name	Scientific name	Abbreviation
Black-capped Chickadee	*Parus atricapillus*	BCCH
Brown Creeper	*Certhia americana*	BRCR
Chestnut-backed Chickadee	*P. rufescens*	CBCH
Common Raven	*Corvus corax*	CORA
Dark-eyed Junco	*Junco hyemalis*	DEJU
Evening Grosbeak	*Hesperiphona vespertinus*	EVGR
Golden-crowned Kinglet	*Regulus satrapa*	GCKI
Gray Jay	*Perisoreus canadensis*	GRJA
Hammond's Flycatcher	*Empidonax hammondii*	HAFL
Hairy Woodpecker	*Picoides villosus*	HAWO
Hermit Warbler	*Dendroica occidentalis*	HEWA
MacGillivray's Warbler	*Oporornis tolmiei*	MGWA
Olive-sided Flycatcher	*Contopus borealis*	OSFL
Pine Siskin	*Corduelis pinus*	PISI
Pileated Woodpecker	*Dryocopus pileatus*	PIWO
Red-breasted Nuthatch	*Sitta canadensis*	RBNU
Rufous Hummingbird	*Selasphorus rufus*	RUHU
Steller's Jay	*Cyanocitta stelleri*	STJA
Swainson's Thrush	*Catharus ustulatus*	SWTH
Vaux's Swift	*Chaetura vauxi*	VASW
Varied Thrush	*Ixoreus naevius*	VATH
Warbling Vireo	*Vireo gilvus*	WAVI
Pacific Slope Flycatcher	*Empidonax difficilis*	WEFL
Western Tanager	*Piranga ludovicianus*	WETA
Wilson's Warbler	*Wilsonia pusilla*	WIWA
Winter Wren	*Troglodytes troglodytes*	WIWR

tests were performed at the 0.05 level of significance. A key to bird species codes, common names, and scientific names is provided in Table 1.

RESULTS

Species composition.—Forty-six species were detected during the study. The Brown Creeper, Chestnut-backed Chickadee, Golden-crowned Kinglet, Evening Grosbeak, and Winter Wren were common in all stands during both seasons (Table 2). In addition, Hammond's Flycatcher, Hermit/Townsend's warbler, Swainson's Thrush, and Western Flycatcher were found in all stands during the summer. Because the study was conducted in the zone of hybridization between Hermit and Townsend's warblers, we could not distinguish the two species by song. Vaux's Swift (4 observations) and Black-capped Chickadee (8 observations) were observed

TABLE 2

AVIAN POPULATION DENSITIES (#/40 HA) IN OLD-GROWTH, MATURE, AND YOUNG SERAL STAGES IN THE WESTERN CASCADE MOUNTAINS, OREGON, DURING SUMMER AND WINTER 1984

Species[a]	Old-growth (N = 5)		Mature (N = 5)		Young (N = 2)	
	$\bar{x}$	± 2 SE	$\bar{x}$	± 2 SE	$\bar{x}$	± 2 SE
			Summer			
BRCR	24.10	6.50	9.50	4.50	1.00	1.8**
CBCH	42.00	17.20	33.40	19.20	22.40	11.3*
CORA	0.70	1.20	0.00	0.00	0.70	0.80
DEJU	9.00	9.70	1.60	1.50	26.30	36.90
EVGR	0.10	0.10	0.60	0.30	0.20	0.3*
GCKI	14.30	6.70	12.10	8.00	11.90	14.10
HAFL	30.90	10.60	30.70	10.90	7.40	0.0*
HAWO	0.50	0.50	0.50	0.30	0.50	1.00
HETH	0.90	1.00	0.30	0.20	1.80	2.40
HEWA	5.90	4.70	4.70	2.30	1.70	2.00
MGWA	1.60	3.20	0.00	0.00	8.80	17.70
ROBI	0.10	0.10	0.80	0.80	0.50	0.60
RUHU	66.70	29.80	29.50	31.40	40.00	80.00
STJA	0.80	0.70	1.20	0.90	3.50	2.1**
SWTH	6.50	3.90	14.30	9.70	25.50	3.0*
VATH	3.60	2.00	1.20	1.30	0.00	0.00
WAVI	0.00	0.00	0.00	0.00	11.70	23.30
WEFL	11.70	4.80	12.50	11.30	14.60	0.00
WETA	1.40	1.20	2.20	1.40	5.40	10.70
WIWA	1.90	2.00	3.90	3.50	3.00	0.30
WIWR	39.30	5.00	47.00	13.20	18.80	27.40
Total	261.70	58.50	205.70	43.80	205.30	169.30
			Winter			
BRCR	6.20	2.90	7.50	2.20	3.60	7.10
CBCH	103.20	30.00	91.70	32.20	97.70	77.60
DEJU	3.90	4.50	1.30	2.50	6.00	4.90
EVGR	5.00	4.80	10.90	6.70	92.90	144.0*
GCKI	55.80	11.00	57.40	31.90	72.10	13.60
HAWO	5.40	4.50	2.60	3.30	1.80	3.70
WIWR	171.10	24.00	218.90	88.70	148.30	70.00
Total	350.50	36.90	390.20	81.00	422.30	139.70

[a] Table 1.
* $P < 0.05$, analysis of variance.
** $P < 0.01$, analysis of variance.

only in old-growth stands, and Olive-sided Flycatcher (10 observations) were observed in two old-growth and one mature stand during the summer. Varied Thrush was recorded only in old-growth and mature stands and during summer. Pileated Woodpecker was detected predominately in old-growth and mature forests. Similarly, the Hairy Woodpecker was re-

corded mostly in old-growth and mature forests during winter, but some were observed in one young-aged stand. Twenty-one observations of Warbling Vireos occurred in a single young-aged stand during summer.

Summer densities and species richness.—No major differences in species richness were observed between the three forest types with 26, 29, and 32 species recorded in mature, old-growth, and young stands, respectively. Thirty-nine species of birds were detected in the 12 stands during the summer, of which 21 were observed >15 times to estimate density. Brown Creepers, Chestnut-backed Chickadees, Hermit/Townsend's warblers, Rufous Hummingbirds, and Varied Thrushes had highest densities in old-growth stands (Table 2). Abundances of Brown Creepers and Chestnut-backed Chickadees were significantly ($P < 0.05$) higher in the old-growth and mature forests than in young forests. Abundances of Hammond's Flycatchers ($P < 0.05$), Hermit/Townsend's warblers, and Winter Wrens were similar in old-growth and mature forests and greater than densities in young stands. Common Ravens were equally abundant in old-growth and young stages, but densities were very low, and there was no significant difference among all three seral stages. Numbers of Evening Grosbeaks, Wilson's warblers, and Winter Wrens were highest in the mature stands; but only densities of the Evening Grosbeak were significantly ($P < 0.05$) higher. Species with highest abundance in the young successional stages were Dark-eyed Junco, MacGillivray's warbler, Stellar's Jay, Swainson's Thrush, Warbling Vireo, and Western Tanager. The Warbling Vireo was found only in one young stand and at low numbers. Abundances of Hairy Woodpecker, Golden-crowned Kinglet, and Pacific Slope Flycatcher were similar across all forest types. Abundances of Brown Creeper, Varied Thrush, Chestnut-backed Chickadee, and Hermit warbler were greater with increasing age of forest stands, while numbers of Steller's Jays, Swainson's Thrushes, and Western Tanagers were less with increasing age of forest stands.

Winter densities.—Species richness during winter differed little among the three forest types, with 12, 15 and 15 species recorded in old-growth, mature, and young stands, respectively. Twenty species were recorded in all 12 stands during the winter survey period, and densities could be estimated for seven of these. Except for Evening Grosbeaks, only minor differences in abundance were noted among the three forest types (Table 2). Evening Grosbeak densities were 10–20 times greater ($P < 0.05$) in the young stands as in mature and old-growth forests. Highest numbers were found in the old-growth forests for Chestnut-backed Chickadees and Hairy Woodpeckers, although neither were significantly different among forest types. Abundances of Chestnut-backed Chickadees were high and similar throughout all forest types. Brown Creepers and Winter Wrens

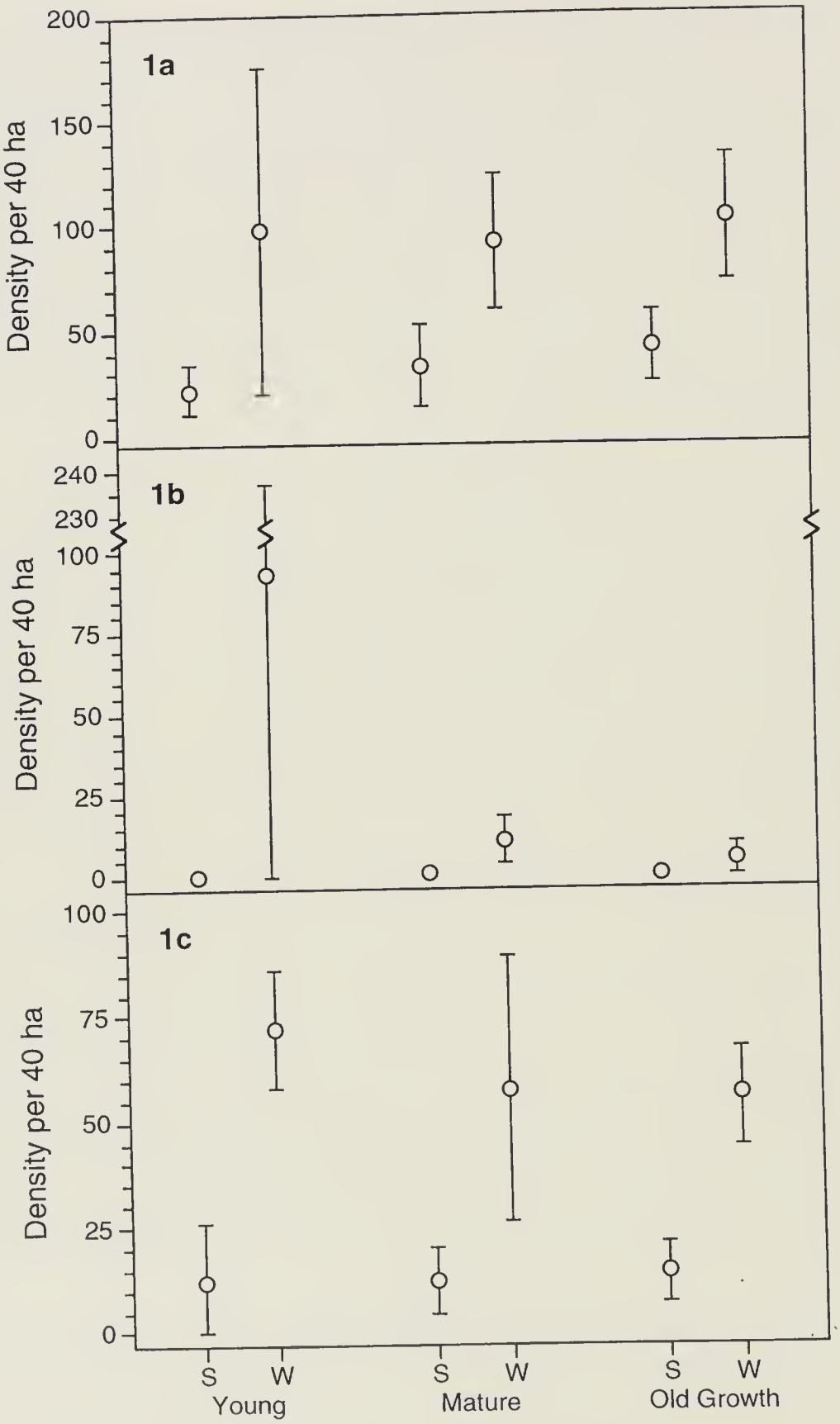
had their highest numbers in the mature forests. Abundances of the Dark-eyed Junco, Evening Grosbeak, and Golden-crowned Kinglet were highest in young forests. Hairy Woodpecker numbers were greater with increased stand age; Evening Grosbeak numbers were less with stand age.

Seasonal changes.—Abundances of Chestnut-backed Chickadees, Evening Grosbeaks, Golden-crowned Kinglets, Hairy Woodpeckers, and Winter Wrens were much higher in winter as compared to summer (Figs. 1, 2). These species are the most common winter residents, and some form large winter flocks. In contrast, numbers of Dark-eyed Junco were generally lower in the winter than in summer (Fig. 2c). All the warblers, flycatchers, and thrushes were not present on the study area during winter because they migrated out of the area.

DISCUSSION

Overall, population densities were highest in old-growth stands during summer and young stands during winter. These results are different from those of Manuwal and Huff (1987) for the Washington Cascades where species richness and abundance were greater in old-growth versus young forests during winter. Birds present in the summer period were, for the most part, breeders, and the greater structural diversity of vegetation in the old-growth forests likely provided more nesting and foraging habitat, resulting in greater abundance. Total overall bird numbers for the three successional stages were approximately twice as high during the winter as compared to the summer. This was likely a result of "flocking" of migrants from higher elevations and latitudes, and there could be more seed- and fruit-bearing vegetation in young stands.

Brown Creepers were relatively more abundant in old-growth stands than in young and mature stands during summer; they were more abundant with increasing age of stands. This is consistent with other studies (e.g., Thomas 1979, Verner 1980, Mannan 1982). Fidelity to old-growth was not as great during winter, as Brown Creeper numbers were similar in both old-growth and mature stands. We found highest numbers of Varied Thrushes in old-growth stands during summer, and they were totally absent from the young stands. Varied Thrushes appear to reach their highest breeding densities in older coniferous forests (Ramsden et al. 1979, Mannan 1982). We observed greater abundances of Chestnut-backed Chickadees and Golden-crowned Kinglets in old-growth forests. These results compare well with findings by Hagar (1960), Buckner et al. (1975), and Manuwal (1991) who found both species to prefer the late-successional forests. We found Hammond's Flycatchers equally abundant in the old-growth and mature forests and four times greater than in the young stands during the summer, which is consistent with the reports of


1a
1b
1c
Density per 40 ha
200
150
100
50
0
240
230
100
75
50
25
0
100
75
50
25
0
S
W
S
W
S
W
Young
Mature
Old Growth

Hagar (1960), Verner (1980), McMillan and Walter (1981), and Manuwal (1991) for Douglas-fir forests. However, Mannan (1982) found Hammond's Flycatcher densities to be equal for both 85 and >200-year-old stands in mixed-conifer forests in northeastern Oregon. Evening Grosbeaks were found at consistently low numbers (<1/40 ha) during summer but were significantly more abundant in mature stands. They were about 100-fold more abundant during winter with highest densities found in young stands. Our results are consistent with those of Thomas (1979) and McMillan and Walter (1981) who found that Evening Grosbeaks breed in dense stands of older conifer forests and move to younger forests during winter. Winter Wrens were most abundant in three mature stands during both seasons, and all of these sites were at low elevations and contained much shrub cover. Hagar (1960) also found Winter Wren densities to be highest in mature stands, while Peterson and Peterson (1983) stated that slash and brush cover positively influenced Winter Wren densities, not age class.

In summary, the results of this study provide information on species that attain their highest densities in small riparian areas of late-successional forests (>120 yrs old) or are found predominately in old-growth forests. During summer, Brown Creepers, Varied Thrushes, Hermit/Townsend's warblers, and Chestnut-backed Chickadees were more abundant with increasing age of stands. Hammond's Flycatchers were more abundant in old-growth and mature forests and much less common in young forests, Evening Grosbeaks were most abundant in mature forest stands. Vaux's Swifts, Black-capped Chickadees, Olive-sided Flycatchers, and Pileated Woodpeckers were not abundant enough to estimate densities, but most observations of these species were in old-growth stands. Likewise, numbers of Hairy Woodpeckers were greater with age of forest stands during winter.

Of the above list of species, the Brown Creeper, Chestnut-backed Chickadee, Black-capped Chickadee, Evening Grosbeak, Varied Thrush, and Hairy Woodpecker are common and widely distributed species, so any dependencies on late-successional forests are unlikely. However, the group contains a number of cavity-nesting species (Chestnut backed Chickadee, Black-capped Chickadee, Brown Creeper, Vaux's Swift, and Pileated Woodpecker) that may be responding to higher densities of snags

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FIG. 1. Densities of Chestnut-backed Chickadee (1a), Evening Grosbeak (1b), and Golden-crowned Kinglet (1c) in three forest types during summer (S) and winter (W), western Oregon. Circles and bars represent mean ± 2 SE; where only circles are present, error bars are too small to graph.

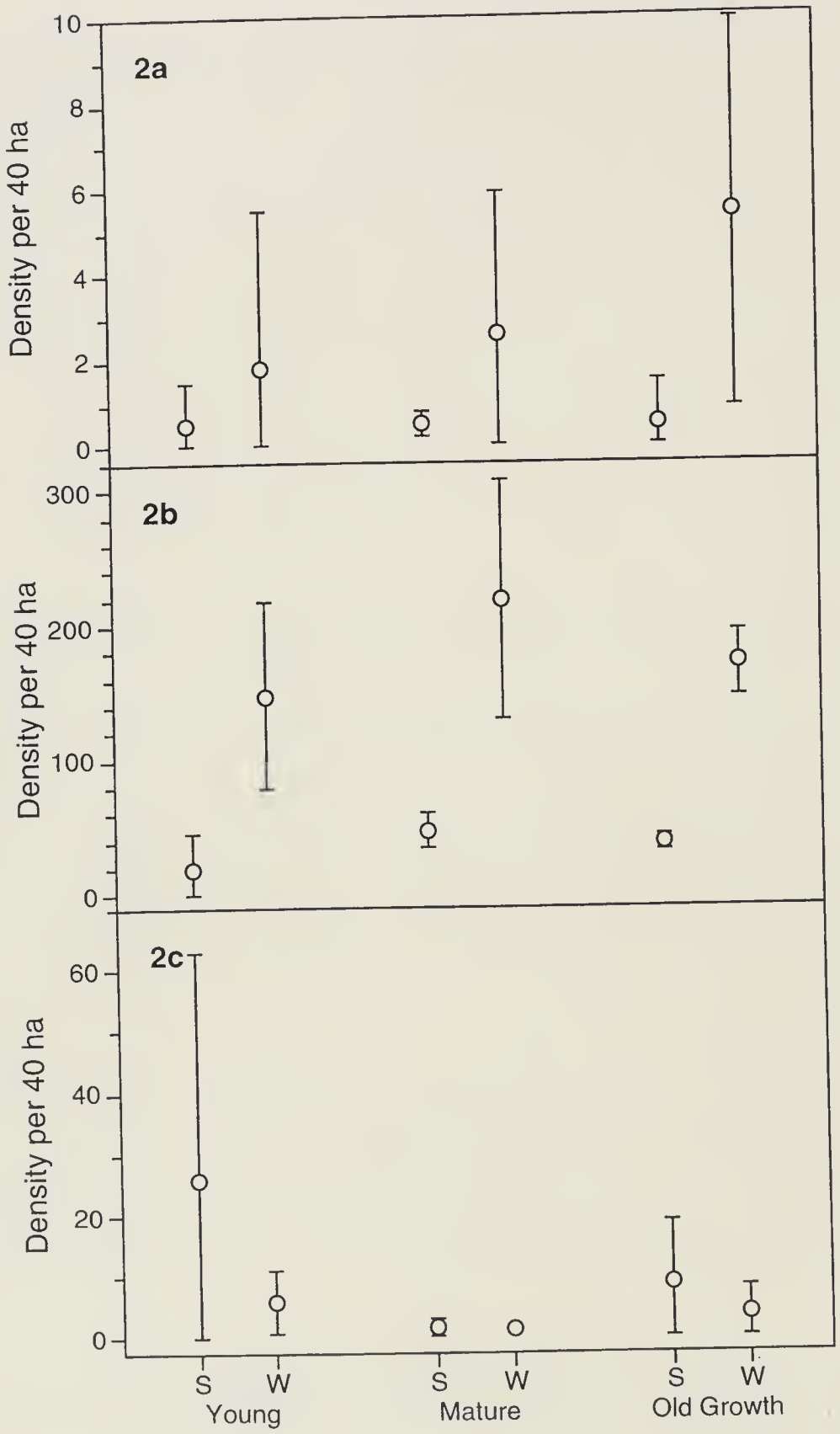
2a
Density per 40 ha
10
8
6
4
2
0
2b
Density per 40 ha
300
200
100
0
2c
Density per 40 ha
60
40
20
0
S
W
Young
S
W
Mature
S
W
Old Growth

TABLE 3

RANKED ABUNDANCE OF BIRD SPECIES IN YOUNG, MATURE, AND OLD-GROWTH FORESTS OF THE OREGON AND WASHINGTON CASCADES

	Young			Mature			Old-growth		
Species[a]	This study	Gilbert and Allwine 1991	Manuwal 1991	This study	Gilbert and Allwine 1991	Manuwal 1991	This study	Gilbert and Allwine 1991	Manuwal 1991
RUHU	1			4			1		
CBCH	4	3	6	2	4	5	2	3	3
WIWR	5	2	2	1	2	1	3	1	1
HAFL	9	4		3	3		4	4	
BRCR	16		9	8		6	5		7
GCKI	7		3	7		2	6		2
WEFL	6	5	4	6	6	4	7	5	4
DEJU	2		5	10		8	8		8
SWTH	3			5			9		
HEWA		1	1		1	3		2	9
RBNU		6	8		5	9			6
VATH			7			7		6	5
PISI			10						
GRJA						10			
VASW									10

[a] See Table 1 for list of common and scientific names of birds.

or logs in late-successional forests. The importance of snags to these species in relation to their association with late-successional forests needs further clarification. Hairy Woodpeckers were the only species that displayed an association with old-growth forests during winter. Based on these findings and the common and widely distributed nature of Hairy Woodpeckers, winter bird surveys in riparian areas are probably not high priority to assess associations with late-successional forests.

Riparian associates—Similar studies on avian communities in upslope habitats have been conducted in young, mature, and old-growth forests in the Oregon Cascades (Gilbert and Allwine 1991), Oregon Coast Range (Carey et al. 1991), and Washington Cascades (Manuwal 1991). These studies provide estimates of relative bird abundance but only qualitative comparisons of ranked abundances can be made (Table 3), because the

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FIG. 2. Densities of Hairy Woodpecker (2a), Winter Wren (2b), and Dark-eyed Junco (2c) in three forest types during summer (S) and winter (W), western Oregon. Circles and bars represent mean ± 2 SE; where only circles are present error, bars are too small to graph.

previous studies did not estimate densities. All the species we detected in riparian areas were also found in upland areas in the above studies so we did not identify any riparian obligate species. However, Swainson's Thrushes and Rufous Hummingbirds were abundant along headwater streams in this study, but were detected infrequently in upland areas in the above studies. Further study may reveal some association with riparian areas for these two species. In contrast, Hermit/Townsend's warblers, Varied Thrushes, and Red-breasted Nuthatches were abundant in upland areas of the above three studies but were not among the top 10 most abundant species in riparian areas in this study. These species may be associated with upland habitats.

ACKNOWLEDGMENTS

This study was funded by the U.S.D.A. Forest Service, Pacific Northwest Research Station, Olympia, Washington. The research was contracted through the Oregon Cooperative Wildlife Research Unit; Oregon State Univ., Oregon Department of Fish and Wildlife, National Biological Service, and Wildlife Management Institute cooperating.

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Wilson Bull., 108(2), 1996, pp. 292–301

HABITAT CHANGES AND SUCCESS OF ARTIFICIAL NESTS ON AN ALKALINE FLAT

MARCUS T. KOENEN,[1] DAVID M. LESLIE, JR.,[2] AND MARK GREGORY[3]

ABSTRACT.—We studied habitat changes and success of artificial ground nests on an expansive alkaline flat at Salt Plains National Wildlife Refuge (NWR), Oklahoma, in 1993 and 1994. Aerial photographs of the refuge taken during 1941–1942, 1966, and 1989 were digitized to evaluate changes of the alkaline flat, herbaceous rangeland, and shrub rangeland that was dominated by saltcedar (*Tamarix* spp.). Vegetation cover increased by about 600 ha between 1941 and 1989, and alkaline flat decreased by >240 ha. Field experiments were conducted to determine predator and flooding impacts on artificial nests that simulated Least Tern (*Sterna antillarum*) and Snowy Plover (*Charadrius alexandrinus*) nests. Experimental nest plots were placed on the alkaline flat adjacent to, 500 m from, and 1000 m from herbaceous rangeland, shrub rangeland, and stream habitat that was not associated with vegetation. Plot comparisons were made by calculating the probability of nest success with a modified Mayfield Method. Nests near vegetation had significantly higher losses to mammalian predators ($P < 0.05$) but significantly lower losses to flooding ($P < 0.05$) than nests at 500 or 1000 m from vegetation. Encroaching vegetation will likely continue to reduce habitat for ground-nesting birds and simultaneously increase predation rates on nests. *Received 20 June 1995, accepted 10 Jan. 1996.*

The interior population of the Least Tern (*Sterna antillarum*) has been listed as endangered since 27 June 1985 (U.S. Fish and Wildl. Serv. 1985). The inland population of the Snowy Plover (*Charadrius alexandrinus*) is currently listed as a Category 2 species (U.S. Fish and Wildl. Serv. 1991), and the coastal population of the Snowy Plover was federally listed as threatened on 5 March 1993 (U.S. Fish and Wildl. Serv. 1993). The population decline of the interior Least Tern has been attributed largely to loss of breeding habitat due to river channelization and construction of impoundments (U.S. Fish and Wildl. Serv. 1990). Snowy Plovers use similar habitat and likely are affected by the same habitat changes that caused the population decline of the interior Least Tern.

An alkaline flat at Salt Plains NWR contains the largest concentration of breeding Least Terns in Oklahoma (U.S. Fish and Wildl. Serv. 1990). Predation and flooding have been identified as the major causes of Least Tern and Snowy Plover egg losses on the flat (Grover and Knopf 1982, Hill 1985, Utych 1993). Coyotes (*Canis latrans*) are the main egg predator, and rain causes sheet flooding on the flat which can wash eggs out of nests.

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Predation and flooding are likely consequences of habitat changes that have occurred at Salt Plains NWR since its creation in the 1930s. Reservoir construction and the spread of saltcedar (*Tamarix* spp.) have altered riparian habitats in the southwestern United States, including parts of Oklahoma (Brock 1994, Stinnet et al. 1987). Several studies have reported higher predation rates on artificial bird nests close to forest-prairie or forest-farmland edge habitats than on nests farther from the edge (Andrén and Angelstram 1988, Burger 1988, Paton 1993, Wilcove et al. 1986), but no studies have examined predation rates on Least Terns and Snowy Plover eggs relative to proximity to vegetated habitat. We assessed habitat changes at Salt Plains NWR and evaluated their impact on predation and flooding of Least Tern and Snowy Plover nests. As our alternate hypotheses, we predicted that predation rates would be higher on nests situated close to vegetation that provides cover for predators than nests farther from vegetation and that nests closer to streams would be more susceptible to flooding losses than nests farther away from streams.

STUDY AREA AND METHODS

Salt Plains NWR is located in Alfalfa County in northcentral Oklahoma and currently contains an alkaline flat of 5095 ha where Least Terns and Snowy Plovers nest (Grover and Knopf 1982, Hill 1985, Utych 1993, Schweitzer 1994). The alkaline flat is closed to the general public except for a small public use area on the southwestern corner of the flat that is open between 1 April and 15 October for collecting selenite crystals (Koenen 1995).

The alkaline flat is nearly level and poorly drained. The water table is at the surface in some areas and up to 1-m deep in others (Williams and Grover 1975). Salt Plains NWR receives an average annual rainfall of 68 cm, of which about 60% occurs in spring and summer. Rain can cause 1–3 cm sheets of moving water on the alkaline flat, which can remain for several hours to several days. Sheet flooding can wash eggs out of nests and submerge entire colonies.

The alkaline flat at Salt Plains NWR is nearly bare; sparse vegetation includes sea purslane (*Sesuvium verrucosum*) and inland salt grass (*Distichlis stricta*). Vegetation forms well-defined borders at the edge of the alkaline flats. The east and south sides of the alkaline flat are dominated by exotic saltcedar; the north and west sides of the alkaline flat are primarily bordered by grazed mixed-grass prairie.

Creeks flow across the alkaline flat into the Great Salt Lake of Oklahoma and are ephemeral and multibranched. The Great Salt Lake was created by a dam across the Salt Fork of the Arkansas River in 1941. The resulting reservoir flooded about 30% of the original 11,137-ha alkaline flat (Purdue 1976).

Least Terns nest in loosely defined colonies along the west branch of the Salt Fork of the Arkansas River, Clay Creek, Cottonwood Creek, and Spring Creek and in scattered patches throughout the alkaline flat (Hill 1985, Schweitzer 1994). The average distance between Least Tern nests is 70 m (Schweitzer 1994). Snowy Plover nests are widely scattered and can be found in Least Tern colonies and areas not used by terns. Nests of both species are shallow scrapes (ca 0.5–4 cm deep × 5–10 cm wide) and typically contain 1–3 eggs (Harrison 1979).

We identified and manually digitized habitat at Salt Plains NWR from 1:16,000 and 1:

20,000 aerial photographs obtained from the Natural Resource Conservation Service, U.S. Dept. of Agriculture, using an Altek graphic digitizer board and GRASS#4.0 (USACERL 1991) Geographical Information System software. Aerial photographs were taken on (1) 24 November 1941 and 22 January 1942, (2) 10 June 1966, and (3) 2 December 1989. The refuge boundary was superimposed over the 1966 photograph, digitized as a separate file, and laid over each digitized habitat map. Digitized habitat (vector) maps were labeled according to major cover types and converted to 30-m resolution raster maps for habitat analyses (Johnson 1993). Cover (ha) was calculated for herbaceous rangeland, shrub rangeland, alkaline flat, and the Great Salt Lake, including an island within Salt Plains NWR's boundary south of Highway 11.

To evaluate the impact of habitat changes and predators on survival of nests of ground nesting birds, we conducted controlled experiments with artificial nests and Japanese Quail (*Coturnix coturnix*) eggs that simulated Least Tern and Snowy Plover nests. Artificial nests were used because we could control nest placement in desired treatment areas. The goal was to identify potential predators, areas sensitive to predation, and areas sensitive to flooding.

In 1993, 60- × 90-m plots were placed adjacent to, 500 m from, and 1000 m from shrub rangeland and the west branch of the Salt Fork of the Arkansas River in the northeastern corner of the alkaline flat (N = 3 plots). In 1994, the experiment was expanded with 15 new plots. A new plot was established about 1000 m north of each of the 1993 plots (N = 3 plots) to replicate assessment of proximity to shrub rangeland. Paired plots were placed about 1000 m from one another and adjacent to, 500 m from, and 1000 m from grazed herbaceous rangeland on the west side of the alkaline flat (N = 6 plots). Similarly, paired plots were placed adjacent to, 500 m from, and 1000 m from Cottonwood Creek, not associated with vegetation cover (N = 6 plots).

Each plot contained 12 artificial nest scrapes placed 30 m apart, and each nest contained 2–3 quail eggs. Eggs were placed in the nests for three 21-day trials (17 May–6 June; 16 June–6 July; and 16 July–6 August) in 1993 and 1994 to imitate the incubation period of Least Terns and Snowy Plovers (Hill 1985). The remaining eggs were removed after each 21-day trial, and scrapes were left empty for 10 days before the beginning of the next trial. Nests were monitored every 3–4 days to determine predation rates and other factors causing nest losses.

Mayfield's method (1975) was used to compare the probability of nest success in each plot. We used a slight modification of the Mayfield method to compare effects of flooding and predation. The Mayfield method determined daily mortality rates and the probability of nest success based on nest failure over the number of days that nests were observed (exposure). Because nest failure may have been the result of flooding, predation, abandonment, or other factors, we modified the Mayfield method to calculate separate rates of daily mortality due to predators (predator mortality) and flooding (flooding mortality). Only clutches lost to predators were considered to have failed when calculating predator mortality. Similarly, only clutches lost to flooding were considered to have failed when calculating flooding mortality. The number of days that ≥one egg remained in nest scrapes was used to determine exposure. Predator and flooding mortality rates were compared among treatments with 95% confidence intervals; significant differences ($P < 0.05$) were demonstrated by non-overlapping confidence intervals (Johnson 1979). Nest success comparisons were made by pooling data for similar treatments (i.e., similar distance from a vegetation type) and trial periods when there were no significant differences.

A nest was considered successful if ≥one egg remained in the nest scrape at the end of the 21-day trial. Nests were considered predated if crushed eggs, large shell fragments, and/or predator footprints were located at a nest. Nests were considered flooded if eggs were

TABLE 1
AERIAL COVERAGE OF DOMINANT HABITAT (HA) AT SALT PLAINS NATIONAL WILDLIFE REFUGE

	1941/1942	1966	1989
Herbaceous rangeland	311	197	336
Shrub rangeland (north)	1546	1853	2142
Shrub rangeland (south)	1044	937	1014
Salt flat	5342	5688	5095
Great Salt Lake	3811	3290	3349
Total area	12,175	12,175	12,175

washed out of nests and relocated in the area. Nests without clear signs of outcome were categorized as unknown and were not included in the final analysis.

RESULTS

Habitat changes.—The refuge boundary south of Highway 11 encompassed 12,175 ha (Table 1). Herbaceous rangeland decreased by 114 ha between 1941 and 1966 and increased by 139 ha between 1966 and 1989. The most dramatic changes occurred on the northeastern side of the refuge where shrub rangeland increased from 1546 to 1853 ha from 1941 to 1966 and increased to 2142 ha between 1966 to 1989. The shrub vegetation spread 12.3 ha/yr between 1941 and 1966 and 12.6 ha/yr between 1966 and 1989. Total herbaceous and shrub rangeland cover increased from 2901 ha in 1941 to 3492 ha in 1989, which represented a 3.4 ha/yr spread from 1941 to 1966 and a 22.0 ha/yr spread from 1966 to 1989. The alkaline flat decreased from 5342 ha in 1941 to 5095 ha in 1989, and the Great Salt Lake decreased 462 ha over the same period. This represented a net loss of 709 ha of alkaline flat and lake cover.

Predator and flooding impact.—In 1993, there were no significant differences ($P > 0.05$) in overall nesting success of artificial nests at various distances from shrub rangeland (Table 2). In 1994, overall nest success adjacent to shrub rangeland (0.42) and adjacent to Cottonwood Creek (0.47) was significantly higher ($P > 0.05$) than nest success in plots 500 m from Cottonwood Creek (0.16) (Table 3). Nest success was not significantly different among plots placed adjacent to, 500 m, and 1000 m from shrub rangeland or herbaceous rangeland. In contrast, nest success was higher adjacent to Cottonwood Creek than 500 m from the Creek.

Coyotes were the only mammalian nest predator positively identified on the salt flats by sight or tracks; however, some tracks may have been from feral dogs (*Canis familiaris*). Canids left distinctive eggshell remains at nests where eggs were eaten; egg remains were similar to those shown

TABLE 2

PROBABILITY OF NEST SUCCESS (MAYFIELD METHOD) AND 95% CONFIDENCE INTERVAL OF ALL NEST PLOTS PLACED AT THREE INTERVALS (0 M, 500 M, AND 1000 M) FROM SHRUB RANGELAND AT SALT PLAINS NATIONAL WILDLIFE REFUGE, OKLAHOMA, IN 1993 (N = 36)

	Shrub rangeland		
	Adjacent to	500 m	1000 m
Overall nest success	0.49[a]	0.37[a]	0.28[a]
Confidence interval (95%)	0.35–0.68	0.25–0.55	0.21–0.50
Nest success based on canid mortality	0.24	0.31	0.15
Confidence interval (95%)	0.08–0.69	0.12–0.79	0.02–1.21
Nest success based on flood mortality	0.52	0.43	0.49
Confidence interval (95%)	0.24–1.09	0.18–0.98	0.23–0.99

[a] Probabilities followed by the same letter are not significantly different among columns; 95% confidence interval comparisons (Johnson 1979).

and discussed by Sooter (1946). Ring-billed Gulls (*Larus delawarensis*) increased substantially on the alkaline flat in late July and August 1993 and 1994. They predated up to 83% of artificial nests in treatment plots, but this was not included in our analysis of predation because they did not predate the relatively few Least Tern and Snowy Plover nests that remained that late in the nesting season (Hill 1985, Schweitzer 1994, Koenen 1995). Therefore, our estimates of predator mortality on artificial nests represented predation by only canids, primarily coyotes.

In 1993, there were no significant ($P < 0.05$) differences in nest success among plots associated with shrub rangeland based on mortality due to canids (Table 2). However, comparison of canid predated plots in 1994 indicated significant lower nest success for plots adjacent to shrub and herbaceous rangelands and within 500 m of herbaceous rangeland than 500 m and 1000 m from shrub rangeland, 1000 m from herbaceous rangeland, and all Cottonwood Creek plots (Table 3).

Losses of artificial nests associated with shrub rangeland due to flooding were not significantly different among plots in 1993 (Table 2). Comparison of flooded nests in 1994 indicated significantly ($P > 0.05$) higher nest success adjacent to shrub rangeland (0.89) than on plots located 500 m and 1000 m from shrub rangeland, 1000 m from herbaceous rangeland, and all Cottonwood Creek plots (Table 3). Plots adjacent to herbaceous rangeland also had higher nest success than plots located 500 m and 1000 m from Cottonwood Creek.

DISCUSSION

The absence of high scouring floods due to flood control by reservoir construction has resulted in dense saltcedar stands in sandy floodplains

TABLE 3

PROBABILITY OF NEST SUCCESS (MAYFIELD METHOD) AND 95% CONFIDENCE INTERVAL OF ALL NEST PLOTS (AND REPLICATES) PLACED AT THREE INTERVALS (0 M, 500 M, AND 1000 M) FROM SHRUB RANGELAND, HERBACEOUS RANGELAND, AND COTTONWOOD CREEK AT SALT PLAINS NATIONAL WILDLIFE REFUGE, OKLAHOMA, IN 1994 (N = 36)

	Shrub rangeland			Herbaceous rangeland			Cottonwood Creek		
	0 m	500 m	1000 m	0 m	500 m	1000 m	0 m	500 m	1000 m
Overall nest success	0.42[a]	0.32[ab]	0.40[ab]	0.29[ab]	0.27[ab]	0.23[ab]	0.47[a]	0.16[b]	0.26[ab]
Confidence interval (95%)	0.30–0.59	0.21–0.48	0.27–0.51	0.18–0.47	0.16–0.42	0.13–0.39	0.34–0.65	0.08–0.28	0.16–0.42
Nest success based on canid mortality	0.39[a]	0.83[b]	0.86[b]	0.38[a]	0.31[a]	0.86[b]	0.78[b]	1.00[c]	0.93[bc]
Confidence interval (95%)	0.29–0.55	0.72–0.97	0.76–0.90	0.27–0.55	0.21–0.47	0.75–0.98	0.65–0.92	—	0.84–1.03
Nest success based on flood mortality	0.89[a]	0.59[b]	0.59[b]	0.69[ab]	0.64[ab]	0.41[bc]	0.49[bc]	0.26[c]	0.36[bc]
Confidence interval (95%)	0.80–0.99	0.45–0.76	0.45–0.76	0.55–0.86	0.50–0.82	0.29–0.57	0.36–0.66	0.16–0.39	0.25–0.55

[a,b,c] Probabilities followed by the same letter are not significantly different among columns; 95% confidence interval comparisons (Johnson 1979).

in the southwestern United States, including Oklahoma (Kerpez and Smith 1987, Stinnet et al. 1987). Sandbars along the Canadian River in western Oklahoma decreased from 68% to 15% of the total floodplain between 1954 and 1983; shrub dominated wetlands increased from 13% to 46%. Schulenberg and Ptacek (1984) noted that encroaching salt cedar on sandbanks in Kansas reduced nesting habitat available to Least Terns.

Vegetation in Least Tern colonies generally does not cover >20% of the ground surface (Thompson and Slack 1982, Gochfeld 1983). Encroaching vegetation and related habitat changes may cause terns to abandon a site (Gochfeld 1983, Burger 1984, U.S. Fish and Wildl. Serv. 1990, Boyd and Rupert 1991, Ziewitz 1992). Saltcedar tolerates the salt levels found on the alkaline flats at Salt Plains NWR (Ungar 1966) and dominated the shrub rangeland that encroached about 709 ha onto the alkaline flat and waterways between 1941 and 1989. The rate of spread on the northeastern alkaline flats was similar from 1941 to 1966 and from 1966 to 1989. Because of the high water table and often saturated soils on the salt flat, the saltcedar-dominated shrub rangeland will likely continue to spread away from the west branch of the Salt Fork of the Arkansas River and onto the alkaline flat. Herbaceous rangeland cover fluctuated slightly between periods analyzed; however, it does not appear to be encroaching onto the salt flat habitat.

Our artificial nest experiment indicated that overall nest success was relatively similar near vegetated or away from vegetated areas. However, causes of nest failure differed among experimental areas. In support of our alternate hyotheses, nests adjacent to shrub rangeland had greatest nest failure from predators in 1994 and areas near streams had highest nest losses due to flooding. However, areas adjacent to a stream with shrub rangeland had lower nest losses due to flooding than areas near a stream with no vegetation. The saltcedar-dominated rangeland may have encroached into these areas because flooding did not regularly occur there. In contrast, dense saltcedar stands also can stabilize substrate and alter fluvial processes (Stinnet et al. 1987). After established, vegetation may have channeled water away from the salt flats or acted as a barrier to sheet flooding. Saltcedar has not become fully established on the west bank of the west branch of the Salt Fork of the Arkansas River; continued saltcedar encroachment may further alter fluvial processes and have positive or negative consequences for ground nesting birds. Accelerated saltcedar growth along the Rio Grande, Pecos, and Gila rivers, for example, stabilized channel sediments, reduced stream velocity, accelerated sedimentation, and increased flood risks (Blackburn et al. 1982).

The increase in shrub rangeland over the last 50 years at Salt Plains NWR likely increased habitat favorable for canids and their predation of

tern and plover nests. Coyotes have been implicated as major nest predators of Least Tern and Snowy Plover nests at Salt Plains NWR; about 5 to 60% of monitored nests have been lost to predators annually between 1977 and 1994 (Grover and Knopf 1982, Hill 1985, Utych 1993, Koenen et al. 1996). Artificial nests may not be as vulnerable to predation as real nests (Angelstram 1986, Andrén and Angelstram 1988, Martin 1987, Willebrand and Marctström 1988, Paton 1993); however, there was no significant difference in the rate of canid predation of artificial nests and real nests in our study (Koenen 1995). Because of similarity between artificial nests and real nests, we contend that management must account for the different factors that cause nest losses on different areas of the alkaline flat. Nesting areas near vegetated areas should receive greater protection from predators, while areas farther from vegetation should be managed to minimize effects of flooding (Koenen et al. 1996). Long-term management plans also should consider vegetation control to maintain nesting areas, reduce impact of predators, and monitor changes in flooding potential.

ACKNOWLEDGMENT

We thank S. L. Gale Koenen, K. A. Shannon, and S. Smith, for checking nest plots and the G. M. Sutton Avian Research Center and hundreds of Coturnix Quail for donating eggs. We greatly appreciate comments on an earlier draft of this paper from F. Knopf, P. Hendricks, and two anonymous reviewers. Appreciation also is extended to the refuge personnel, particularly manager R. Krey, for their immense and gracious support. Funding for this study was provided by Region 2 of the U.S. Fish and Wildlife Service, Salt Plains NWR, and the Oklahoma Cooperative Fish and Wildlife Research Unit (U.S. Nat. Biol. Serv., Okla. Dept. Wildl. Conserv., Okla. State Univ., and Wildl. Manage. Inst., cooperating).

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Wilson Bull., 108(2), 1996, pp. 302–316

NESTING ECOLOGY OF SCISSOR-TAILED FLYCATCHERS IN SOUTH TEXAS

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ABSTRACT.—We examined nest-site selection and nesting success of the Scissor-tailed Flycatcher (*Tyrannus forficatus*) on the Rob and Bessie Welder Wildlife Foundation Refuge, San Patricio County, Texas in 1992–1993. Mesquite (*Prosopis glandulosa*) comprised 22% of available shrubs; however, Scissor-tailed Flycatchers used shrubs out of proportion to their availability, placing 91% of their nests in mesquite. Scissor-tailed Flycatcher nests were placed in taller shrubs with less vertical cover and patchiness, with less total horizontal cover, and with greater heterogeneity than in random sites. The majority of nests were oriented to the northwest (18%), north (17%), and northeast (23%). Successful nests were in shrubs with less vertical patchiness and horizontal cover and with greater vertical cover (≤1 m) and horizontal heterogeneity than unsuccessful nests. Nest-site selection appeared to be a tradeoff between orienting nests to provide protection from abiotic factors while minimizing horizontal cover to allow sufficient visibility for nest defense. *Received 7 April 1995, accepted 1 Dec. 1995.*

Nest-site selection is closely tied to fitness (Martin and Roper 1988) by influencing losses caused by predators and weather. Tyrant flycatchers (*Tyrannus* spp.) breed later (Robins 1970) and have longer nesting cycles than most other open-nesting passerines. Except for three species of phoebes (*Sayornis* spp.), the Vermilion Flycatcher (*Pyrocephalus rubinus*), and the Acadian Flycatcher (*Empidonax virescens*), most flycatchers raise only one brood per year (Bent 1942, Robins 1970, Murphy 1989). Scissor-tailed Flycatchers (*T. forficatus*) tend to have the largest clutch size among the tyrannids (Murphy 1989), slower growth rates for nestlings, and more time spent in the nest (Murphy 1988). Scissor-tails breed throughout the south-central United States, with the core nesting range being located in north-central Texas (Fitch 1950). Like other flycatchers, Scissor-tailed Flycatchers typically place nests in relatively conspicuous locations, often near the canopy edge (Bent 1942) and at heights ranging from 1.5 to 12.2 m (Fitch 1950). Scissor-tailed Flycatchers tend to forage and nest along roadways in open prairies dotted with few trees (Bent 1942). Use of roadways and ditches by mammalian predators may render Scissor-tailed Flycatcher nests more susceptible to predation as well as increasing the possibility of predation on adults while foraging. The inherently greater diversity of snakes and avian predators in southern lati-

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tudes may impose an additional cause of potential nest failure. These factors, combined with the intense heat, high winds, heavy rainfall, and high humidity typical of the summer months in south Texas, are predominant factors influencing the environment and, therefore, nesting success. This leads to the prediction that Scissor-tailed Flycatchers have evolved specialized nest placement to mitigate these influences. Scissor-tailed Flycatchers should select the largest available shrubs within an area as nest sites because tall shrubs with greater volume facilitate placement of nests at locations inaccessible to terrestrial predators, provide protection from abiotic factors, and allow for nest defense from reptilian and avian predators and avian nest parasites.

Our objectives were to quantify nesting ecology and to test the hypothesis that nest-site selection and nesting success of the Scissor-tailed Flycatcher is a positive function of vertical cover and a negative function of horizontal cover of the nest shrub. Predictions based on this hypothesis were that (1) successful Scissor-tailed Flycatcher nests are placed in shrubs with greater vertical cover than shrubs containing unsuccessful nests; (2) successful nests are placed in shrubs with less horizontal cover than at unsuccessful nests; and (3) nests are placed within shrubs at locations inaccessible to mammalian and reptilian predators, i.e., a negative relationship should exist between relative nest height and relative horizontal distance of nest from main stem to shrub canopy.

STUDY AREA AND METHODS

We eonduеted this study on the Rob and Bessie Welder Wildlife Foundation Refuge whieh eneompasses 3156 ha and is 80 km northeast of Corpus Christi in northern San Patrieio County, Texas. The primary habitat assoeiated with the study area was a mesquite-mixed grass eommunity (Drawe et al. 1978) and was eomposed of moderately dense stands of honey mesquite interspersed with dense elusters of ehaparral and interstitial areas of grass. Other eommon brush speeies inelude huisaehe (*Acacia smallii*), spiny haekberry (*Celtis pallida*), agarito (*Berberis trifoliata*), lotebush (*Ziziphus obtusifolia*), and lime prieklyash (*Zanthoxylum fagara*). The soil assoeiated with the mesquite-mixed grass eommunity is Vietoria elay (0–1% slope). Prevailing winds are from the southeast and may reach average speeds of 56 km/h (Guekian and Gareia 1979). Peak periods of rainfall oeeur during April, May, and June.

We found Seissor-tailed Flyeateher nests from May through August 1992 and 1993 by traversing pastures and by using an extensive network of unimproved roads. Nests were loeated by observing Seissor-tailed Flyeatehers and by visually inspeeting shrubs. We marked nests, using floreseent flagging plaeed on a shrub or strueture adjaeent to the nest shrub, and we revisited at three-day intervals, reeording the number of eggs and/or young at eaeh nest to determine nest fates. An extendible mirror-and-pole deviee was used to view the eontents of nests. Evidenee of nest sueeess ineluded observations of young fledging from a nest or the presenee of young near a nest. Nests were eonsidered sueeessful if ≥ 1 nestling fledged. Failure was assumed when nest eontents disappeared before the anticipated fledging date or when the nest was damaged or blown out of the shrub. Not all nests were

found before the onset of egg-laying or incubation; therefore, success was quantified by using Mayfield's method (Mayfield 1961, 1975) to compensate for exposure. We tested for a difference in nest success between years with an *F*-test (Johnson 1979).

Nest sites were revisited to conduct vegetation measurements following fledging of young or upon nest failure. Since some nests were lost because of abiotic factors or predation or because some nests were inaccessible, only 60 nest sites were measured. Vegetation measurements were also taken at randomly selected sites (N = 30 each year) to represent available nest sites. Available shrubs were selected by pacing 100 m in a random direction from each Scissor-tailed Flycatcher nest site and then choosing the shrub nearest the end of the 100-m distance. We recorded shrub species and determined proportions of each species at used and at available sites for preference/avoidance analysis. Frequency of nest placement among available shrubs was compared using chi-square analysis. If a chi-square test resulted in rejecting the null hypothesis that a species was used in proportion to availability, a Bonferroni *z*-statistic was used (Neu et al. 1974) to estimate whether a Scissor-tailed Flycatcher selected or avoided that shrub species.

Variables were grouped into two levels of resolution: nest placement within the shrub and vertical and horizontal structure of the nest shrub to six m from the nest (Table 1). A 6-m-radius from the nest was selected to describe horizontal structure, since most nests were in uniform habitats composed of mesquite trees with canopies <10 m in diameter. We quantified horizontal and vertical structure (cover) and patterning (patchiness) of the vegetation using a method similar to the "bird centered view" described by (Weins and Rotenberry 1985). We quantified vertical and horizontal cover using a 2-cm diameter rod marked at 0.1 m increments. We recorded the number of 0.1 m increments touching vegetation out of the total possible number of increments within each of three height (vertical) or distance (horizontal) classes (0–1 m, 1–3 m, and 3–6 m). For example, within the 1–3 m class (a distance of 2 m) there were 20 possible increments. If vegetation touched 10 of the 20 increments, cover was 50%. Vertical cover was measured by extending the rod from the ground to the canopy projecting through the nest. Horizontal structure was quantified by extending the rod parallel to the ground, at nest height, in each of the four cardinal directions from the nest. Cover was calculated from the mean of the four cover estimates within each of the three distance classes. If the nest was too high to be reached from the ground or it could not be reached by climbing the tree, a ladder was used to measure horizontal cover. At the nest placement level, we determined average three-dimensional cover surrounding the nest. The structure rod was oriented vertically to nest height and structure measurements were recorded at 0.5-m increments moving away from the nest in each of the four cardinal directions. Mean percent cover was determined within each of three distance classes (0–1 m, 1–3 m, and 3–6 m) horizontally from the nest and extending from the ground to the outer canopy of the shrub. The coefficient of variation (CV) for structure variables represented an index of the patchiness of the measured variable. We also calculated a horizontal heterogeneity index (HHI) (Rotenberry and Weins 1980) using horizontal structure data.

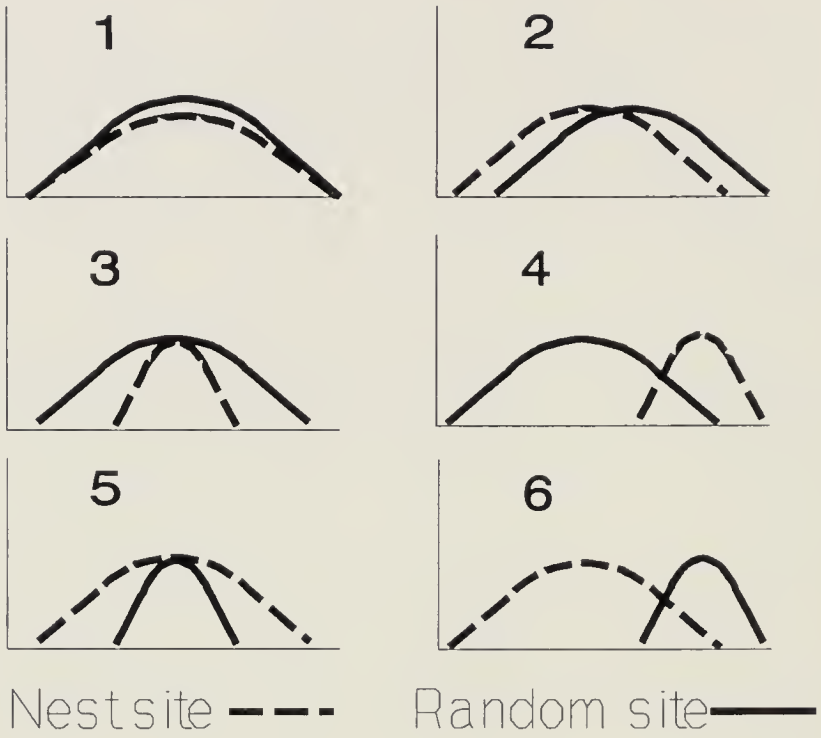
We compared means and variances for statistical differences between nest sites and random sites and between successful and unsuccessful nests to explore the relationship between nest success and nest-site selection, (Ratti et al. 1984). Homogeneity of variance tests can indicate aspects of nest-site selection not readily detectable by comparing sample means alone. We considered nest-site selection to have occurred when (1) Scissor-tailed Flycatchers selected nest-site characteristics with different means but similar variance as random sites, (2) nest sites had similar means but less variance than at random sites, and (3) nest sites had different means and less variance than at random sites (Fig. 1). In the second situation, traditional comparisons of sample means would not have detected habitat selection, whereas,

TABLE 1

MEASURED AND CALCULATED VEGETATION VARIABLES USED TO QUANTIFY NEST SITES AND AVAILABLE RANDOM SITES

Variable	Description
Shrub characteristics[a]	
TOTHT	Total height of the shrub (m)
VI	Shrub vigor (1 = ≤25%, 2 = 26 ≤ 50%, 3 = 51 ≤ 75%, 4 = 76 ≤ 100%) based on the percent of living material
NSDIAM	Average diameter of the shrub at nest height (m)
NSVOL	Shrub volume (*pi*/3) (NSDIAM*NSDIAM*TOTHT/2) (m^3)
VCOV01	Vertical cover projected through nest from 0–1 m (%)
VCOV13	Vertical cover projected through nest from 1–3 m (%)
VCOV36	Vertical cover projected through nest from 3–6 m (%)
TVCOV	Total vertical cover 0–6 m (%)
CVVCOV	Coefficient of variation (CV) for the three vertical cover variables
HCOV01	Average horizontal cover 0–1 m from nest (%)
HCOV13	Average horizontal cover 1–3 m from nest (%)
HCOV36	Average horizontal cover 3–6 m from nest (%)
THCOV	Total horizontal cover (%)
CVHCOV	Coefficient of variation (CV) for the three horizontal cover variables
HHI	Horizontal heterogeneity
AVEDNW	Average distance to the nearest shrub (m)
CVDNW	Coefficient of variation (CV) of distance to the nearest shrub in each of the four compass directions
Placement characteristics	
NESTHT	Height of nest (m)
RELHT	Ratio between nest height and total height of shrub
TOPDIST	Vertical distance from nest to canopy of shrub (m)
ORIENT	Orientation of the nest within the shrub (degrees)
DTRK	Horizontal distance from the main stem to the nest (m)
TOTTRK	Distance from main stem to the canopy through nest (m)
RELDIST	Relative horizontal distance of nest between main stem and shrub canopy
NSTANGL	Angle of main branch supporting nest (degrees)
COV01	Three dimensional cover from 0–1 m around the nest (%)
COV13	Three dimensional cover from 1–3 m around the nest (%)
COV36	Three dimensional cover from 3–6 m around the nest (%)
TCOV	Total cover in a 6-m radius cube around the nest (%)
CVCOV	CV for the three cover measurements

[a] All shrub variables were used to compare flycatcher nests and random sites.



	Mean value	
Variance	not different	different
not different	1. no selection	2. selection
less at nest site	3. selection	4. selection
less at random site	5. no selection	6. no selection

FIG. 1. Possible combinations of means and variances at nest sites and random sites that indicate habitat selection or random choice.

an instance when sample means were different but variance was less at random sites would not indicate habitat selection.

Treatment means (nest vs random, successful vs unsuccessful) for nest-site variables were compared with a completely random design and a two-way factorial treatment structure with the general linear model (GLM) procedure (SAS 1988). When an interaction occurred between years, contrasts were used to compare treatments by year. Percentage or proportional data were arc-sine transformed before statistical analyses (Sokol and Rohlf 1973). Analyses were performed with SAS (Statistical Analysis Institute 1988) and conclusions were based on $\alpha = 0.05$ unless otherwise indicated.

RESULTS

Reproductive success.—Forty-eight nests were monitored during 1992–1993, resulting in 789 nest-days of observations (Table 2). The first nest-

TABLE 2
ESTIMATES OF NEST SUCCESS, CONFIDENCE INTERVALS, AND SOURCES OF NEST FAILURE FOR SCISSOR-TAILED FLYCATCHERS BREEDING

	1992	1993
Nest days	186	603
Number of eggs ($\bar{x} \pm$ SD) (N)	4.4 ± 0.5 (12)A	4.5 ± 0.5 (19)A
Number of young ($\bar{x} \pm$ SD) (N)	3.2 ± 1.6 (7)A	3.0 ± 1.0 (10)A
Daily mortality rate	5.9%	2.2%
Mayfield estimate (N)	94.1% (17)	97.8% (31)
95% confidence interval	90.6–97.6%	96.6–99.0%
Probability of survival to fledging	15.6%A	50.7%B
95% confidence interval	4.9–26.3%	34.8–66.6%
Sources of nest failure		
Weather (N)	45.5% (5)	7.7% (1)
Predation (N)	36.4% (4)	15.4% (2)
Abandonment (N)	18.1% (2)	7.7% (1)
Unknown (N)	0.0% (0)	69.2% (9)

[a] Means followed by the same letter are not significantly different ($P > 0.05$).

ing activity was recorded on 5 May 1992 and 3 May 1993. Egg laying began on 28 May 1992 and 25 May 1993. Mean fledging dates respectively were 1 July 1992 (N = 7) and 3 July 1993 (N = 10). Based on complete nests, the number of eggs/nest and number of fledglings/nest did not differ ($P \geq 0.05$) between years (Table 2). Nineteen nests were destroyed during storms or were removed (used as nesting material) by other birds before vegetation could be quantified. These and all other nests that could not be visually inspected because they were inaccessible were excluded. Of the remaining 48 nests (17 in 1992, 31 in 1993) used to calculate success, 31 were found before initiation of egg-laying. Probability of nesting success was greater ($P = 0.03$) during 1993 than 1992. Nest success was 39% when years were pooled. There was a year × nest success interaction for the number of eggs/nest ($P = 0.03$) and for the number of young/nest ($P = 0.0001$) between successful and unsuccessful nests. Both the number of eggs/nest ($P = 0.09$) and the number of young/nest were similar ($P = 0.06$) at successful and unsuccessful nests during 1992. Number of eggs/nest and young/nest were greater ($P = 0.01$, $P = 0.0001$, respectively) at successful nests than at unsuccessful nests during 1993.

Rainfall during 1992 (128.4 cm) and 1993 (102.8 cm) was above the annual average of 88.9 cm for the Welder Refuge and therefore may not reflect average conditions. Abiotic factors accounted for the largest percentage (46%) of nest failures in 1992. All five nests lost to abiotic factors

were found on the ground near the shrub following storms. Predation accounted for 36% of nest failures, and the remaining 18% of failures were because of abandonment. Predation was assumed when nest contents disappeared under suspicious circumstances, i.e., eggs or young disappeared between consecutive visits or when contents disappeared following observations of predators near the nest site. In 1993, the majority (69%) of nest failures were because of unknown causes.

Frequency of shrub selection.—Scissor-tailed Flycatcher nests (N = 60) were placed nonrandomly among the available shrub species ($\chi^2 = 170.46$, df = 4, $P < 0.0001$). Frequency of available shrubs in the habitat was mesquite (22%), huisache (20%), spiny hackberry (18%), lime pricklyash (20%), brazil (*Ziziphus obtusifolia*) (8%), agarito (5%), Texas persimmon (*Diospyros texana*) (3%), sugar hackberry (*Celtis laevigata*) (2%), and wolfberry (*Lycium berlandieri*) (2%). Scissor-tailed Flycatchers selected mesquite and avoided all other shrubs during 1992 and 1993. Ninety-one percent of the nests (N = 55) were placed in mesquite. Nests were also placed in huisache (N = 1), lime pricklyash (N = 2), sugar hackberry (N = 1), and under a transformer on a telephone pole (N = 1).

Nest-site characteristics.—Nests were placed 2.8 ± 0.8 m high and 1.9 ± 1.0 m ($\bar{x}$ ± 1 SD; N = 60) from the main stem of the shrub. Relative height of the nest within the shrub and relative horizontal distance from main stem to the shrub canopy were 0.60 ± 0.11 and 0.49 ± 0.18, respectively. There was no correlation ($r = -0.15$, $P = 0.26$) between relative nest height and relative horizontal distance. Average height, diameter, and volume of nest shrubs were 4.7 ± 0.9 m, 7.6 ± 2.7 m, and 172.0 ± 133.0 m^3, respectively. Mean nest orientation was to the southeast; however, a majority (58%) of nests were oriented northwest (18%), north (17%), and northeast (23%) (Fig. 2).

Flycatcher vs random comparisons.—Thirteen of the 17 vegetation characteristic means differed ($P < 0.05$) between flycatcher nests and random sites (Table 3). The year × treatment (used or random) interaction was significant ($P = 0.0001$) for total horizontal cover. Total horizontal cover was greater ($P < 0.05$) at random sites than at nest-sites during 1992 but was not different ($P > 0.05$) during 1993. Scissor-tailed Flycatchers chose shrubs that were taller ($P < 0.001$), greater in diameter ($P < 0.001$) and volume ($P < 0.001$), and had less ($P < 0.001$) variation in vertical cover than random shrubs. They also chose shrubs with less vertical cover from 0–1 m ($P < 0.001$), from 1–3 m ($P = 0.001$), and from 0–6 m (total vertical cover) ($P \leq 0.001$). However, there was more ($P < 0.001$) vertical cover from 3–6 m at their nests than at random shrubs. Scissor-tailed Flycatchers selected sites that were more ($P = 0.002$) open, i.e., a greater distance to the nearest shrub and shrubs that were patchier

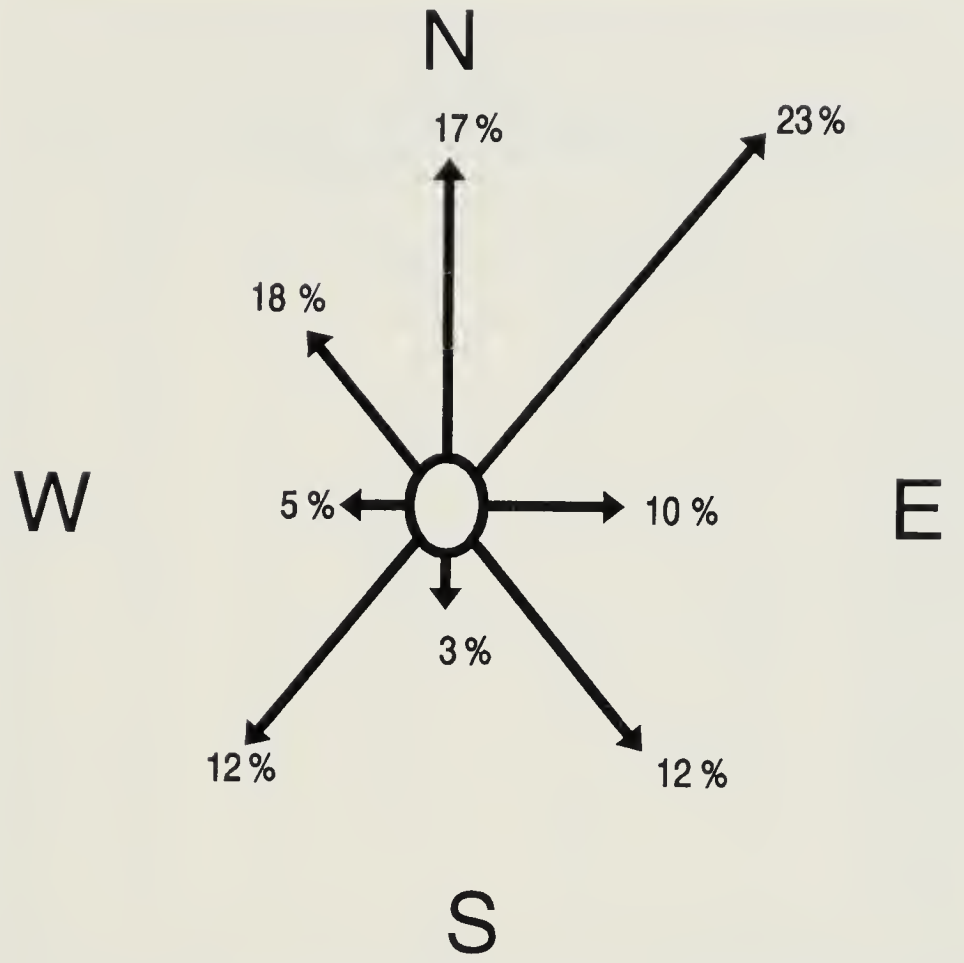


FIG. 2. Percent of Scissor-tailed Flycatcher nests (N = 60) oriented within each of the eight cardinal compass directions on the Rob and Bessie Welder Wildlife Refuge, 1992–1993.

($P < 0.001$), i.e., greater variation in the amount of horizontal cover, than random sites. Nests were also placed in shrubs with greater ($P < 0.001$) horizontal heterogeneity than random sites.

Tests for homogeneity of variance indicated differences ($P < 0.05$) for seven characteristics (Table 3). Scissor-tailed Flycatchers selected shrubs with greater variation in shrub diameter ($P < 0.001$) and volume ($P < 0.001$) than random shrubs. Random shrubs had greater ($P < 0.001$) variance for vertical cover from 0–1 m, from 1–3 m and for total vertical cover, with less ($P < 0.001$) variance for vertical cover from 3–6 m than shrubs selected by flycatchers. The variance of average distance to the nearest woody vegetation was greater ($P < 0.001$) at nests than at random sites.

Successful vs unsuccessful nest comparisons.—There was no difference ($P > 0.05$) between relative height or relative horizontal distance at suc-

TABLE 3

COMPARISON OF VEGETATION CHARACTERISTICS AT SCISSOR-TAILED FLYCATCHER NESTS (N = 60) VS RANDOM SITES (N = 60)

Variable	Flycatcher		Random		Ho: equal means *P*-value	Ho: equal variance *P*-value
	$\bar{x}$	SD	$\bar{x}$	SD		
Shrub characteristics						
TOTHT*	4.7	0.9	2.0	0.9	0.000	0.841
V1	3.3	0.9	3.6	0.7	0.051	0.060
NSDIAM	7.6	2.7	2.0	1.5	0.000	0.000
NSVOL	172.0	133.0	10.3	27.0	0.000	0.000
VCOV01*	0.23	0.15	0.70	0.26	0.000	0.000
VCOV13*	0.19	0.12	0.39	0.30	0.001	0.000
VCOV36	0.33	0.17	0.04	0.10	0.000	0.000
TVCOV*	0.25	0.08	0.39	0.15	0.000	0.000
CVVCOV*	64.4	33.4	108.2	40.0	0.000	0.170
HCOV01	0.53	0.27	0.59	0.21	0.199	0.083
HCOV13	0.37	0.21	0.34	0.27	0.345	0.075
HCOV36*	0.20	0.25	0.26	0.23	0.037	0.466
THCOV*[a]	0.32	0.20	0.41	0.19	0.000	0.674
CVHCOV*	73.5	43.0	65.4	38.0	0.000	0.351
HHI*	1.7	0.6	1.0	0.5	0.000	0.239
AVEDNW	13.8	24.7	3.8	2.4	0.002	0.000
CVDNW	40.0	25.2	47.1	26.9	0.129	0.624

[a] Significant ($P < 0.05$) interaction between year and treatment (used and random). THCOV at used and random sites differed ($P < 0.0001$) for 1992 and was similar ($P = 0.6545$) for 1993.

* Habitat selection.

cessful and unsuccessful nests. Analysis of cover measurements at Scissor-tailed Flycatcher nests indicated vertical cover from 0–1 m was greater ($P = 0.036$) at successful nests (Table 4). Successful nests were also placed in shrubs with less ($P = 0.013$) patchiness of vertical cover than unsuccessful nests. The year × treatment (nest success) interaction was significant ($P < 0.05$) for horizontal cover from 1–3 m and from 3–6 m and for total horizontal cover. Contrasts indicated that three cover attributes at successful and unsuccessful nests differed for 1993 ($P < 0.05$) but not for 1992 ($P > 0.05$).

Tests for homogeneity of variance indicated differences for four characteristics (Table 4). Successful nests were placed in shrubs with less variation in vertical cover from 0–1 m ($P = 0.027$), CV of mean distance to the nearest shrub in each of the four cardinal compass directions ($P = 0.005$), and horizontal heterogeneity ($P = 0.005$). Variance for average distance to the nearest shrub ($P = 0.009$) was greater at successful nests.

TABLE 4

COMPARISON OF VEGETATION CHARACTERISTICS AT SUCCESSFUL (N = 17) AND UNSUCCESSFUL (N = 39) SCISSOR-TAILED FLYCATCHER NESTS ON THE ROB AND BESSIE WELDER WILDLIFE REFUGE, SAN PATRICIO COUNTY, TEXAS, 1992–1993

Variable	Successful		Unsuccessful		Ho: equal means *P*-value	Ho: equal variance *P*-value
	$\bar{x}$	SD	$\bar{x}$	SD		
Shrub characteristics						
TOTHT	4.6	0.8	4.7	0.9	0.220	0.668
V1	3.4	1.0	3.2	0.9	0.801	0.648
NSD1AM	7.7	2.7	7.7	2.7	0.426	0.939
NSVOL	173.0	128.0	175.0	137.0	0.368	0.797
VCOV01*	0.29	0.12	0.21	0.16	0.036	0.027
VCOV13	0.20	0.12	0.18	0.11	0.342	0.953
VCOV36	0.31	0.15	0.33	0.18	0.172	0.131
TVCOV	0.27	0.06	0.24	0.09	0.218	0.231
CVVCOV*	48.8	25.7	71.6	32.6	0.047	0.304
HCOV01	0.45	0.25	0.56	0.27	0.200	0.811
HCOV13*[a]	0.33	0.22	0.39	0.21	0.003	0.686
HCOV36*[a]	0.15	0.19	0.24	0.28	0.000	0.153
THCOV*[a]	0.26	0.16	0.36	0.22	0.000	0.232
CVHCOV	73.6	49.0	72.5	42.5	0.812	0.453
HHI*	1.6	0.3	1.8	0.6	0.285	0.005
AVEDNW	17.9	34.6	12.7	20.8	0.401	0.009
CVDNW*	37.4	14.8	40.6	29.3	0.776	0.005
Placement characteristics						
NESTHT	2.8	0.9	2.8	0.8	0.176	0.643
RELHT	0.60	0.13	0.60	0.11	0.409	0.326
TOPDIST	1.8	0.6	1.9	0.5	0.912	0.373
ORIENT	171.0	68.0	113.0	68.0	0.066	0.867
DTRK	1.7	1.1	2.1	1.0	0.466	0.900
TOTTRK	3.8	1.4	3.9	1.4	0.426	0.939
RELTRK	0.46	0.21	0.50	0.18	0.775	0.243
NSTANGL	37	27	31	22	0.483	0.324
COV01	0.27	0.07	0.23	0.08	0.066	0.326
COV13	0.23	0.06	0.23	0.07	0.140	0.672
COV36	0.20	0.13	0.19	0.11	0.208	0.394
TCOV	0.24	0.06	0.23	0.06	0.279	0.685
CVCOV	32.7	35.7	31.8	25.1	0.463	0.077

[a] Significant ($P < 0.05$) interaction between year and treatment (successful and unsuccessful). HCOV13, HCOV36, and THCOV at successful and unsuccessful nests differed ($P < 0.05$) during 1993 but were similar ($P > 0.05$) during 1992.
* Habitat selection.

DISCUSSION

The nesting success rate (39%) for Scissor-tailed Flycatchers on the Welder Refuge was less than that reported for other flycatchers except Eastern Kingbirds (25.6%) in Kansas (Murphy 1986). Scissor-tailed Flycatchers had the highest success rate 81% (N = 16) (Murphy 1983) and clutch size 4.69 (N = 16) (Murphy 1988) of all tyrannids reported. Mean clutch size on the Welder Refuge was similar to that reported by Murphy (1988), suggesting Fitch's (1950) estimate of nest success was low, possibly because of the inclusion of incomplete nests. Similarities between clutch sizes indicate nests on the Welder Refuge suffered a greater mortality rate during the post-laying period. Above-average rainfall during the 1992 and 1993 breeding seasons was partially responsible for lower nesting success because high winds and heavy rains dislodged nests from shrubs. Murphy (1986) reported losses caused by weather were mostly from wind blowing nests from trees. Abiotic factors were also believed to have accounted for many of the nest failures from unknown causes during 1993. However, since most of the these nests could not be found, or the nest contents had disappeared, the exact cause of failure remains uncertain.

Nest success may be affected at two spatial scales: habitat in the immediate vicinity of the nest (shrub characteristics) and habitat surrounding the nest (characteristics of the nest patch) (MacKenzie and Sealy 1981, Martin and Roper 1988). This study focused on nesting success and nest-site selection at the nest shrub scale. We believe this degree of resolution was sufficient to describe nest-site selection by Scissor-tailed Flycatchers. Nests were placed, on average, 2.8 m high in shrubs 4.7 m tall. Mean height of available shrubs was only 2 m and therefore would not provide much horizontal obstruction for their nests placed in adjacent shrubs. Because of the nest height, conspicuous nest placement, and orientation away from prevailing winds, it appears that Scissor-tailed Flycatchers select attributes related to nest shrubs rather than the surrounding habitat.

Site selection for Scissor-tailed Flycatchers may have been a function of selecting characteristics that allowed adults to monitor and defend the nest site since horizontal cover was less at successful nests. Ricklefs (1977) found that a strong correlation existed between nest conspicuousness and intensity of nest defense in tropical passerines. Scissor-tailed Flycatcher nests were generally found >100 m apart and were located in open stands of mesquite on the Welder Refuge. Fitch (1950) noted that nests were never found within 76 y of each other. Spacing of Scissor-tailed Flycatcher nests is partially a function of the open habitat selected and partially because of the size and aggressive defense of individual

territories. Placing nests in open shrubs (less vertical and horizontal cover) would allow for sufficient air space in which the birds can maneuver to attack intruders. However, less total cover may also increase the risk of nest failure from abiotic factors.

Nest orientation relative to the center of the shrub should influence losses of nests because of abiotic factors, including prevailing southeast winds and numerous thunderstorms originating in the Gulf of Mexico during the nesting season. Since only 25% of the nests were oriented to the east, southeast, or south (toward prevailing winds), the birds appeared to place nests so as to minimize the effects of abiotic factors. Placement of Scissor-tailed Flycatcher nests within shrubs appeared to minimize horizontal cover while favorable nest orientation may have provided some respite from the wind, rain, and sun, thus partially mitigating the effects of mortality from overexposure to the sun. Murphy (1985) described nestling deaths from overexposure to sun in Eastern Kingbirds, as a source of mortality.

Murphy (1983) noted that predation was the driving force behind nest-site selection in Eastern Kingbirds, as nests placed extremely low or extremely high within trees had the lowest probability of fledging young. He added that maximum success occurred at relative nest heights and relative horizontal distances from the tree center to the shrub canopy edge of about 0.5. Our results differ somewhat from the above. Although nests were placed at relative heights and horizontal distances of 0.6 and 0.5, respectively, there was no difference between successful and unsuccessful nests for either variable.

Nest concealment was greater at low predation nests than at high predation nests for woodland birds including the Hermit Thrush (*Hylocichla guttata*), Prairie Warbler (*Dendroica discolor*), Mourning Dove (*Zenaida macroura*), and Eastern Kingbird (Murphy 1983, Westmoreland and Best 1985, Martin and Roper 1988). Great-tailed Grackles (*Cassidix mexicanus*) appeared to be the primary avian predator of Scissor-tailed Flycatcher nests. Large groups of grackles were observed harassing Scissor-tailed Flycatchers at their nest sites on numerous occasions. Raccoons (*Procyon lotor*), and opossums (*Didelphis virginianus*) were the only common mammalian predators present on the study site capable of depredating the flycatcher nests. We documented no incidence of mammalian predation on nests during the two years of this study; however, these mammalian predators are nocturnal and direct observations would be unlikely. Vertical cover ≤ 1 m was greater at successful nests than at unsuccessful nests. Greater ground cover may inhibit some terrestrial predators from locating nests, although reptilian predators may actually benefit.

Nineteen nests were abandoned before egg-laying for unknown reasons.

Frequent visitation to nests has been documented to affect nesting success. However, daily intrusions, including removal of young for measurements, did not adversely affect nesting success of Scissor-tailed Flycatchers (Fitch 1950). Because nests of unknown fate were often found intact although empty, snake predation likely contributed to nest failure. Had mammalian and avian predators been responsible, it is likely that shell fragments or other signs would have been left at the nest site. Several species of snakes known to prey on eggs and nestlings were present throughout the study area. Kingsnakes (*Lampropeltis* spp.), yellow-bellied racers (*Coluber constrictor flaviventris*), and western coachwhips (*Masticophis flagellum testaceus*) were observed at nest sites on several occasions and were observed or suspected to be the source of nest failure on numerous other occasions for Dickcissels (*Spiza americana*), Mourning Doves, Northern Mockingbirds (*Mimus polyglottos*), and Northern Cardinals (*Cardinalis cardinalis*) on the Welder Refuge (Nolte, pers. observ.).

Strength of attachment of the nest to the shrub may be an important component of nest success. Many nests failed before hatching or fledging because they were dislodged from the nest shrub following storms. Conspicuous placement of nests may render them more vulnerable to unpredictable, heavy rainfall and wind events than those of most other passerines which nest in short, dense shrubs in south Texas. Additional research should be conducted to determine if the firmness of nest attachment is related to nesting success.

On the Welder Refuge, randomly available shrubs appeared to be of insufficient size to accommodate placement of flycatcher nests. Mesquite seemed to afford the best compromise by providing optimal cover and by allowing nests to be placed at locations inaccessible to terrestrial predators. Previous investigators have reported that Scissor-tailed Flycatchers nest in any species of tree that is isolated and is open-foliaged (Bent 1942, Fitch 1950). The structural attributes provided by mesquite may be only partially responsible for nest-site selection by Scissor-tailed Flycatchers. They selected for total height of nest shrubs; therefore, size relative to other available shrubs may also have a role in shrub selection on the Welder Refuge.

Based on the results of this study, we accept the hypothesis that Scissor-tailed Flycatchers select nest sites based on horizontal structure of the shrub. Our results indicate that nest-site selection in Scissor-tailed Flycatchers appears to be a trade-off between providing air space around the nest (less horizontal cover) for defense from predators and at the expense of increasing exposure to abiotic influences such as wind, rain, and solar radiation. Results did not, however, support the predictions that nest-site

selection was a function of vertical cover or that a negative relationship existed between relative nest height and relative horizontal distance within the nest shrub.

About 400,000 ha of rangelands in Texas are annually treated with herbicides, often with the goal of decreasing the density of mesquite. Brush management practices, to one degree or another, result in setting back succession. We found evidence that Scissor-tailed Flycatchers show shrub-specific site tenacity. In 1993, six nests were placed in shrubs that contained a Scissor-tailed Flycatcher nest in 1992. Subsequent observations in 1994 indicated that 25 nests were in shrubs containing Scissor-tailed Flycatcher nests in at least one of the two previous years. If areas used as nest-sites are subsequently altered via some brush management practice, returning pairs of Scissor-tailed Flycatchers may attempt to re-nest in dead shrubs. We documented eight occasions when nests were placed in shrubs that were dead before initiation of nesting activity, and in all eight cases the nests failed. The widespread use of such practices could decrease the available nesting habitat for Scissor-tailed Flycatchers. Our results indicate this will undoubtedly result in a greater rate of nest mortality. Other passerine species, including cavity nesters or those that require larger shrubs for nest placement and support, could be equally affected. Managers should consider leaving strips or patches of untreated brush when large acreages of rangeland are managed. Another management strategy could be to leave dispersed mature mesquite in an area following treatment. Brush control on sites without mesquite should allow for the preservation of individuals or loose clumps of the largest trees available.

ACKNOWLEDGMENTS

We are grateful to James Teer and the Rob and Bessie Welder Wildlife Foundation for support during this study. We thank P. A. Moody for assisting with field work and data management. We also thank Fred Guthery, Eric Hellgren, Ralph Bingham, Michael T. Murphy, Richard Conner, and several anonymous reviewers for valuable comments on this manuscript. This is Rob and Bessie Welder Wildlife Foundation contribution 447.

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Wilson Bull., 108(2), 1996, pp. 317–334

BREEDING BIOLOGY OF THE BROWN NODDY ON TERN ISLAND, HAWAII

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ABSTRACT.—We observed Brown Noddy (*Anous stolidus pileatus*) breeding phenology and population trends on Tern Island, French Frigate Shoals, Hawaii, from 1982 to 1992. Peaks of laying ranged from the first week in January to the first week in November; however, most laying occurred between March and September each year. Incubation length was 34.8 days (N = 19, SD = 0.6, range = 29–37 days). There were no differences in breeding pairs between the measurements of the first egg laid and successive eggs laid within a season. The proportion of light- and dark-colored chicks was 26% and 74%, respectively (N = 221) and differed from other Brown Noddy colonies studied in Atlantic and Pacific oceans. The length of time between clutches depended on whether the previous outcome was a failed clutch or a successfully fledged chick. Hatching, fledging, and reproductive success were significantly different between years. The subspecies (*A. s. pileatus*) differs in many aspects of its breeding biology from other colonies in the Atlantic and Pacific oceans, in regard to year-round occurrence at the colony, frequent renesting attempts, large egg size, proportion of light and dark colored chicks, and low reproductive success caused by inclement weather and predation by Great Frigatebirds (*Fregata minor*). *Received 31 Mar., 1995, accepted 5 Dec. 1995.*

The Brown Noddy (*Anous stolidus*) is the largest and most widely distributed of the tropical and subtropical tern species (Cramp 1985). The breeding biology of the nominate subspecies *A. s. stolidus* has been studied extensively in its Atlantic range (Dorward and Ashmole 1963, Robertson 1964, Morris and Chardine 1992); however, few studies exist for *A. s. pileatus* which ranges over most of the Pacific and Indian oceans (Cramp 1985). Brown (1973, 1977) published most of the information on Brown Noddies breeding in the Hawaiian Islands; however, his observations spanned only two breeding seasons. Here, we present observations of the breeding biology of this species in the Northwestern Hawaiian Islands, the northern-most part of its range, and compare it to previous reports from other Hawaiian Islands and with observations of the biology of the subspecies *A. s. stolidus* in the Atlantic Ocean.

STUDY AREA AND METHODS

French Frigate Shoals is a crescent-shaped atoll situated approximately midway in the Hawaiian Archipelago (23°45′N, 166°17′W) and is part of the Northwestern Hawaiian Islands National Wildlife Refuge administered by the U.S. Fish and Wildlife Service (USFWS). The atoll contains 10 well-established islands and as many as nine sandy islets that are seasonally awash (Fig. 1). Tern Island, located near the northwestern tip of the atoll,

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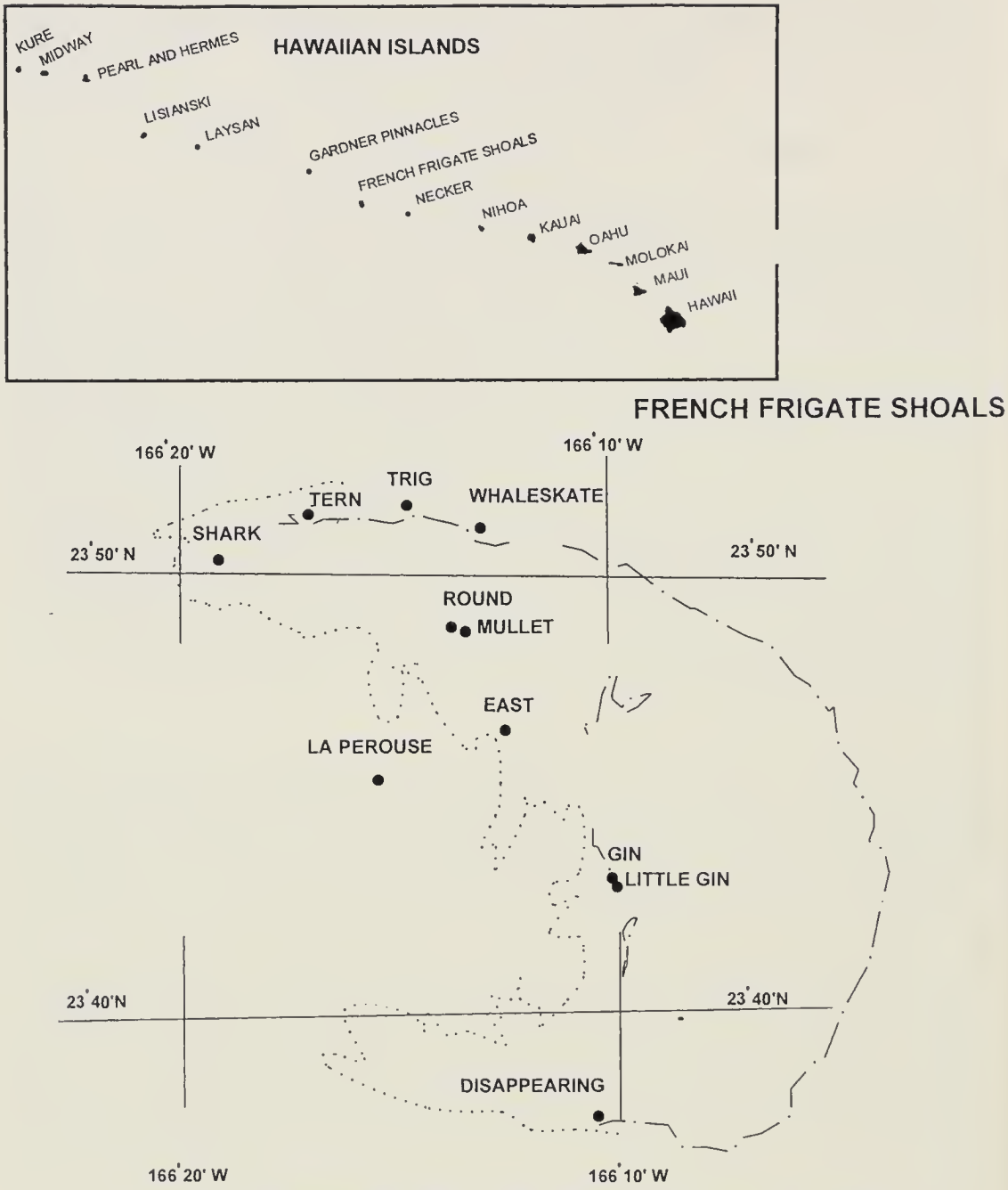

FIG. 1. French Frigate Shoals, with insert of the Hawaiian Islands.

is the largest island and the only human-made island at French Frigate Shoals. Originally 4.4 ha in size, the island is now approximately 15.0 ha, measuring 945 m in length and 99.1 m wide (Amerson 1971, USFWS unpubl. data). The island was expanded to accommodate military operations during the 1940s. An active, crushed-coral runway, approximately 76.2 m wide, extends the length of the island. Sixteen species of seabirds nest on Tern Island (Amerson 1971, USFWS). No mammalian land predators occur within the atoll. At French Frigate Shoals, Brown Noddies nest on Tern, La Perouse, Whaleskate, East and Little Gin islands. Tern Island has the largest nesting colony, with approximately 1700–

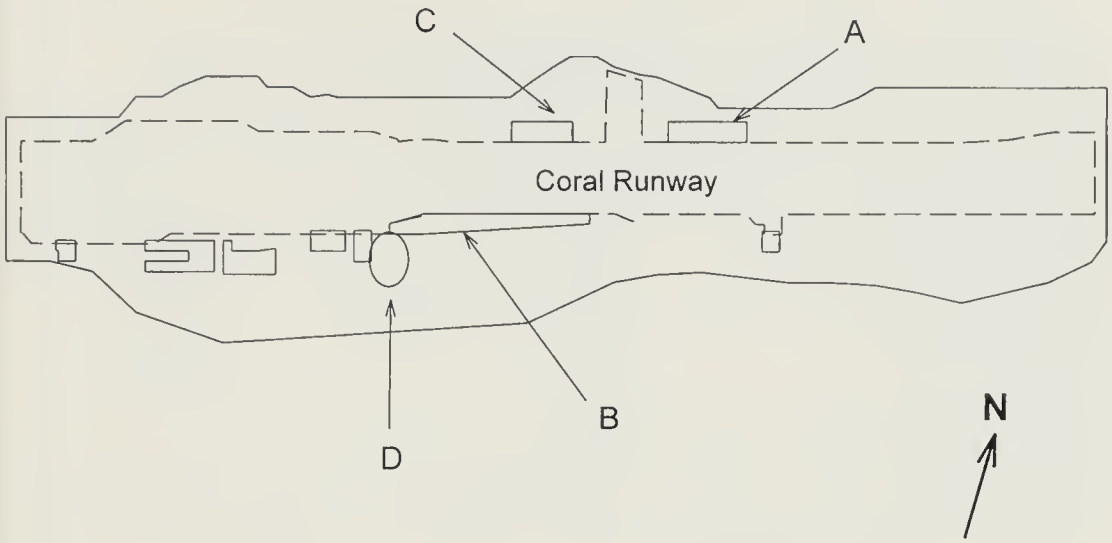

FIG. 2. Location of Brown Noddy study plots A, B, C, and D on Tern Island, French Frigate Shoals, Hawaii.

2500 nesting pairs. East Island, approximately 13 km southeast of Tern Island, is the next largest colony with approximately 500 breeding pairs.

Four study plots were chosen on Tern Island because of high numbers of accessible Brown Noddy nests (Fig. 2). Study plot A occurred on the north side of Tern Island. The plot measured 78 m in length and ranged from 10.3 to 7.8 m wide. The plot consisted of non-vegetated areas of coralline rubble, dense stands of the grass *Lepturus repens* on its northern edge and sparse patches of small *Chenopodium oahuense* shrubs on its southern edge; two small *Tournefortia argentea* bushes were in the middle of the plot. Study plot B was on the south side of the island, extending 120 m east to west and 3.5 m north to south from the edge of the runway. Small (<2 m in height) *Tournefortia argentea* bushes, *Lepturus repens, Boerhavia repens, Portulaca* spp., and *Eleusine indica* were the major vegetative cover in study plot B. A coralline berm extended along the plot's length, approximately 1.5 m from the north edge of the plot. Habitat and total area of study plot C were similar to that of study plot A. Study plot D was used to determine breeding success of Brown Noddy nests >1 m above the ground in *Tournefortia argentea* and *Pluchea* spp. bushes. Study plot A was used in all years of the study, while study plot B was used in 1989–1992; plots C and D were used in 1980, 1981, and 1982.

We made observations of Brown Noddy breeding phenology and population trends on Tern Island from 1982 to 1992. Data on other aspects of breeding biology, including incubation behaviors, egg measurements, chick polymorphism and growth, and parental care and breeding success were collected in 1980–1982 and 1989–1992 (Table 1). Observations in 1980 through 1987 were made by several U.S. Fish and Wildlife Service personnel; observations in 1988–1992 were made primarily by the senior author.

Beginning each breeding season, from 1982 to 1992, we conducted island-wide searches and recorded dates of first arrival for Brown Noddy adults, first eggs laid, and first chicks hatched and fledged. Because of protracted laying and numerous nesting attempts, only the minimum number of breeding pairs on the island was determined each breeding season by recording the highest number of nests containing either an egg or a chick on island-wide monthly counts of nests during 1982–1985 and by island-wide counts made every 36 days (the mean incubation length of Brown Noddies reported by Brown [1977]), during 1985–

TABLE 1
DATA COLLECTION ON TERN ISLAND, FRENCH FRIGATE SHOALS, HAWAII

Data collected	Year collected	Study plot[a]
Breeding phenology	1982–1992	Island-wide
Number of breeding pairs	1982–1992	Island-wide
Incubation behaviors	1980–1981, 1989–1992	A, B, C, D
Egg morphometrics	1980–1982, 1989–1992	A, B, C, D
Chick polymorphism	1980–1981, 1988	A, C, D
Chick growth	1980	A, C, D
Relay intervals	1989–1992	B
Parental care of nestling	1989–1992	B
Breeding success	1982, 1989–1992	A, B, C, D

[a] Study plots C and D were primarily used only in 1980 and 1981 and in 1982 for breeding success.

1992. Study plots were checked every other day while nests were active, and every five days when there were no active nests, except during inclement weather (winds exceeding 8.6 km/h in combination with rain). Because laying occurs throughout the year on Tern Island but is extremely synchronous for noddies, we defined breeding season as the period between the laying of the first egg to the laying of the last egg within the study plots, regardless of calendar year. In 1980 and 1981, breeding occurred from March to October. However, from November 20, 1988 to October 7, 1990, Brown Noddies nested continuously. We considered the beginning of the 1990 breeding season to be December 21, 1989, when there were no chicks less than four weeks of age left on the island and within the plots and when a new peak of laying occurred. From this peak, study plot A was monitored continuously for three successive breeding seasons, December 21, 1989 to October 7, 1990, March 15 to September 10, 1991, and February 2 to November 12, 1992. In 1980 and 1981, all nests within study plots A, C, and D were marked with individually numbered metal tags, and the fate of each nest was recorded. In 1989–1992, nesting success in study plot A was observed by marking each nest with a blue-painted piece of coral placed 5–12 cm north of the nest. For all of study plot A, the total number of new eggs, eggs lost, and newly hatched chicks were recorded at each check. All chicks that reached three weeks of age were banded with a size 3 incaloy USFWS band. All dead chicks found within the plot were recorded.

Beginning in October 1989, breeding adults were color-banded within study plot B to monitor individual breeding success and effort. Twenty-one pairs were banded during 1989. All breeding attempts for these color-banded pairs were recorded. Thereafter, pairs were captured at the beginning of each season so that the number of breeding attempts for each pair could be monitored for the entire breeding season. Thirteen pairs were banded in 1990, and 29 pairs were banded in 1991. All birds were captured by hand, or by using a long-handled minnow net during daytime hours. They were then banded with a unique color-band combination consisting of three plastic bands and a size 3 incaloy, USFWS band. A total of 114 birds, representing 62 pairs, were color-banded.

All nests within study plot B belonging to color-banded pairs were marked with a uniquely numbered rock. Dates of laying, hatching, fledging, and chick departure from the island for each nesting attempt were recorded. Eggs in marked nests were weighed with a 100-g Pesola scale to the nearest 1 g; eggs three days of age or older were not weighed. Measurements of egg length and breadth were taken with digital or manual vernier calipers to the nearest

0.1 mm. The fate of each marked nest was recorded (i.e., failed egg or dead chick). In addition to daily searches, observations of color-banded birds were conducted from May 1 to May 27, 1992 at 06:00–07:45, 12:00–13:45, and 20:00–21:45 h. All sightings of color-banded birds on any part of the island were recorded during 1989–1992. Incubation lengths were gathered periodically throughout 1989–1992 for nests with known dates for laying and hatching. Incubation shifts were followed for a total of 10 pairs in 1980 and 57 pairs in 1981; one bird from each pair was marked on the crown with picric acid. Incubation shifts were recorded every 2 h for a total of 72 h during each of five observation periods. The sex was not known for any of the 67 pairs of birds, and pairs were in various stages of incubation at the time of monitoring.

Proportions of chicks with light down versus dark down were determined in 1980, 1981, and 1989. Although there were intermediate plumages, chicks were considered light-colored if they did not contrast markedly with the coralline rubble and dark if they resembled the color of the adult plumage. In 1980, chick growth for an initial sample of 28 chicks in study plot A was measured every 3–4 days until chicks fledged. Chicks were weighed with a Pesola scale to the nearest 0.5 g; culmen, wing chord, and tarsus lengths were measured with vernier calipers to the nearest 0.1 mm. In 1989–1992, fledglings were weighed (≥one week post-fledging) using a 500-g Pesola scale to the nearest 2.0 g, and culmen and wing chord were measured with vernier calipers to the nearest 0.1 mm. In all years of study, chicks were considered fledged at the first sign of sustained flight when nests were being checked. Island-wide searches for fledglings were conducted, and their nests were checked periodically after dusk between 19:00 and 22:00 h. After 14 days of no sightings, a fledgling was considered absent from the island.

RESULTS

Breeding phenology and population estimates.—The minimum nesting population on Tern Island appeared to increase during the ten years of the study from at least 375 pairs in 1982 to at least 2410 pairs in 1992. Breeding phenology varied widely between years (χ^2 = 15824.28; df = 88; $P < 0.001$); however, the largest peaks of laying occurred between March and September each year (Fig. 3). Peaks of laying varied widely during these months from 1982 through 1985 and in 1991; while in 1986 and 1987, peak laying occurred in late April, and in late June in 1992. From 1988 through 1989, Brown Noddies nested continuously.

Noddies usually nested on the ground in open, coralline rubble areas. Nests varied, ranging from inornate to elaborately lined with pieces of colored plastic, shells, crab carapaces, and vegetation. Brown Noddies nested as high as 1.0 m above the ground in *Pluchea* spp., *Chenopodium ohauense,* and *Lepturus repens,* in which nests consisted of dense platforms of vegetation as large as 0.5 m in diameter and 20 cm thick.

Egg measurements, incubation behaviors, and renesting.—Of 2,889 nests observed on Tern Island, all contained one egg that ranged in color from all white to heavily speckled brown. There was little variation in mean egg length and breadth between years (N = 304 and 303, respectively); however, egg mass differed in some years (N = 253;, one-way ANOVA, Table 2). Mean length, breadth, and mass of color-banded pairs'

FIG. 3. Nesting phenology and numbers of nests containing eggs of Brown Noddies on Tern Island, French Frigate Shoals, Hawaii, 1982–1992.

TABLE 2
MEAN EGG MEASUREMENTS (±SD; N IN PARENTHESES) FOR TERN ISLAND BROWN NODDIES

Year	Length (mm)	Breadth (mm)	Mass (g)
1981	53.7 ± 2.0 (30)	36.9 ± 1.0 (30)	36.0 ± 2.4 (30)
1982	53.4 ± 2.2 (150)	36.7 ± 1.2 (149)	37.2 ± 3.0 (124)
1989	53.3 ± 1.5 (20)	36.6 ± 1.6 (20)	38.2 ± 2.5 (2)
1990	53.2 ± 1.8 (94)	36.9 ± 0.9 (49)	39.0 ± 2.7 (48)
1991	53.2 ± 2.1 (55)	36.8 ± 1.1 (55)	37.9 ± 3.0 (49)
F[a]	0.28	0.53	7.89
P	0.89	0.71	<0.001[b]

[a] ANOVA tests for differences between years; df = 4, 299, for length; 4, 298, for breadth; and 3, 247, for mass.
[b] Egg mass in 1990 differed significantly from 1981 and 1982; in 1991 egg mass differed significantly from 1981; 1989 was not compared due to small sample size.

first eggs were not different from eggs laid later in the same season ($F_{2,102}$ = 0.29, P = 0.02 and $F_{2,83}$ = 2.63, respectively; $P > 0.05$ for all three measures).

Incubating noddies shifted more frequently in the morning (02:00–08:00 h) and night (20:00–02:00 h) than in the midday (08:00–14:00 h) and evening (14:00–20:00 h) (N = 67; χ^2 = 31.5; df = 3; $P < 0.001$), with adults averaging as much as 2.0 shifts during the night period (Table 3). There was no difference in mean shift length between years, so data were pooled ($F_{4,61}$ = 0.02; $P > 0.05$). Average shift length for 67 pairs during 360 hrs of observation was 11.3 h (SE = 0.9; range = 5.3–25.2 h). Average duration from laying to hatching was 34.8 d (N = 19, SD = 0.6, range = 29–37 d).

Of the total number of pairs, 47.0% (N = 34) and 34.3% (N = 35) renested after the first nest failed in 1990 and 1991, respectively. Thirteen of the renests occurred after the loss of an egg, and 24 occurred after losing a chick; one pair relaid twice after losing a chick on each of the two previous attempts (Table 4). There were no differences in the proportion of pairs that relaid in 1990 compared to 1991 (χ^2 = 1.17; df = 1; $P > 0.05$), nor were pairs more likely to relay after losing an egg versus losing a chick (χ^2 = 1.56; df = 1; $P > 0.05$). Average age of chicks lost among pairs that relaid was 7.1 d (N = 26; SD = 7.1; range = 1–20 d). Further, relay interval lengths (the time from laying the first

TABLE 3

INCUBATION BEHAVIORS FOR BROWN NODDIES ON TERN ISLAND DURING EACH OF FIVE 72-H PERIODS OF OBSERVATION

Year	Mean incubation shift length (hours)	Total number of shifts per pair	Number of shifts per time period[a]			
			Morning	Midday	Evening	Night
1980	10.4 ± 6.7[b] (50)	6.0 ± 2.3[c] (10)	1.6 ± 1.1 (10)	1.5 ± 1.3 (10)	1.6 ± 1.1 (10)	1.3 ± 0.9 (10)
1981						
March	11.1 ± 9.5 (73)	7.7 ± 3.4 (14)	1.9 ± 1.6 (14)	0.4 ± 0.9 (14)	1.5 ± 1.0 (14)	2.3 ± 1.4 (14)
May	12.6 ± 7.9 (57)	6.4 ± 1.9 (15)	1.5 ± 1.1 (15)	1.1 ± 1.2 (15)	1.5 ± 0.9 (15)	1.2 ± 1.1 (15)
June	11.7 ± 7.7 (68)	6.9 ± 1.96 (15)	1.3 ± 1.0 (15)	1.0 ± 0.9 (15)	0.9 ± 1.0 (15)	1.7 ± 1.2 (15)
August	10.5 ± 7.8 (67)	7.2 ± 2.6 (13)	1.3 ± 1.6 (13)	1.2 ± 1.1 (13)	1.4 ± 0.8 (13)	1.6 ± 1.3 (13)
All years	11.3 ± 0.9[d]	6.8 ± 0.7	1.5 ± 1.3	0.96 ± 1.1	1.1 ± 1.0	2.0 ± 1.1

[a] Morning: 02:00–08:00 h; midday: 08:00–14:00 h; evening: 14:00–20:00 h; night: 20:00–02:00 h.
[b] Mean ± SD; number of shifts per observation period in parentheses.
[c] Mean ± SD; number of pairs in parentheses.
[d] Mean ± SE.

egg to laying the replacement egg) were not different whether the pair lost an egg, a chick <1 week of age, or a chick >1 week of age (Kruskal-Wallis, H = 4.11; df = 2, N = 7, 11 and 7, respectively; $P > 0.05$). However, pairs that successfully fledged a chick waited longer to nest again than did pairs that lost an egg or a chick (Kruskal-Wallis, H = 16.08; df = 2; N = 6; $P < 0.001$). These data should be interpreted with caution, however, as the sample sizes were small.

Chick polymorphism, growth and parental care.—There were no differences between years in the proportion of light- and dark-colored chicks in 1980, 1981, or 1989 (N = 221; $\chi^2 = 0.253$; df = 2; $P > 0.05$). Down color for chicks during these three years was 26% light- and 74% dark-colored. For 84 of 160 chicks, average age prior to disappearance from the nest did not differ with respect to color (N = 19 and 65, mean = 9.9 d and 7.5 d, SD = 6.9 and 4.6 for dark and light-colored chicks, respectively).

Average chick mass at one day of age was 28.8 g (N = 29, SD = 3.83); chicks attained average adult mass (200.4 g, N = 122) at 34 d of age. Chick mass increased until 38 d post-hatching and began decreasing on day 43 (Fig. 4). At the end of the measurement period (range = 47–51 d), the average chick mass was 195.8 g (N = 13, SD = 18.39). There

TABLE 4

NUMBER OF RELAYS AND CLUTCH INTERVALS FOR BROWN NODDIES DURING 1990 AND 1991

Number of relays (% of pairs)				Relay interval length according to prior attempt (days)[a]			
None	One	Two	Three	Unhatched	<1 week-old	>1 week-old	Fledgling
41 (59.4)	28 (40.1)	4 (14.3)	1 (3.5)	43.5 ± 26.2[b]	22.7 ± 10.3	33.4 ± 19.5	212.3 ± 37.8
				(31)	(11)	(7)	(6)
				12–87 days	15–49 days	17–65 days	180–279 days

[a] Interval lengths not different except for those pairs fledging chicks ($F = 154.46$, df = 2, $P < 0.05$).
[b] Mean ± SD, (N), range in days.

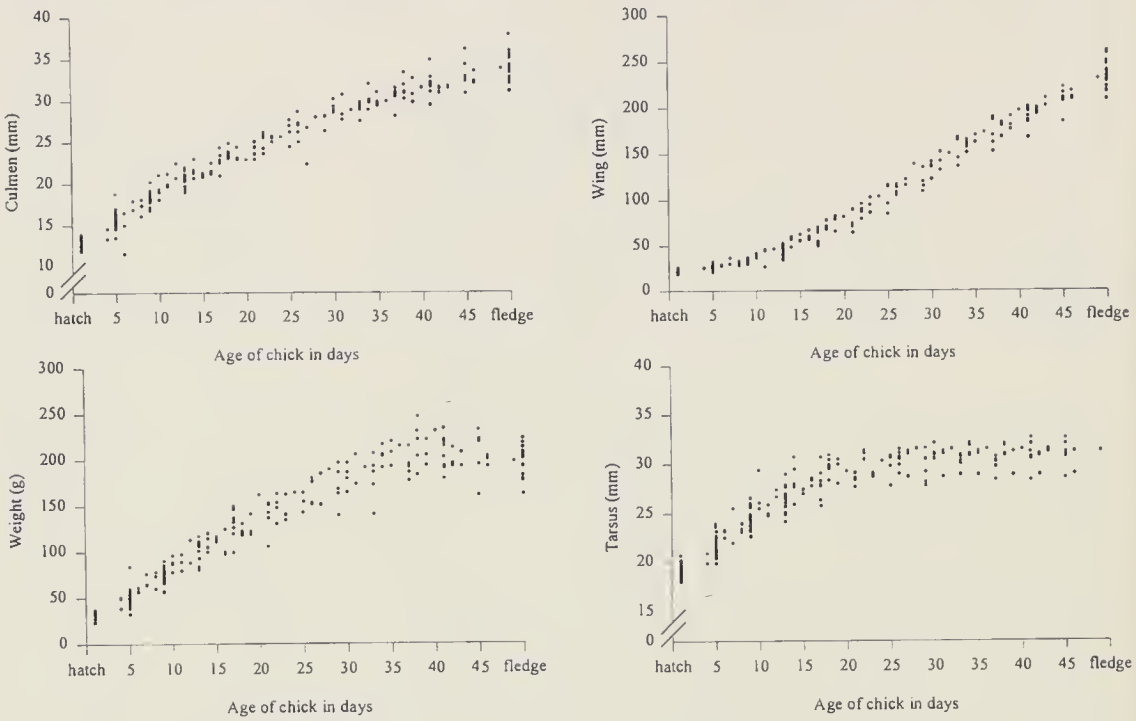

FIG. 4. Growth of Brown Noddy chicks on Tern Island.

was no difference in weight loss between newly fledged chicks and chicks that were weighed ≥ one week post-fledging (t = 1.01, df = 21, P > 0.05). There was relatively little growth in wing length until 10 d of age, followed by steady growth up to 50 d post-hatching, when the measurement period ended (Fig. 4). Culmen length increased throughout the 50 d of measurement, while tarsus length increased until 20 d of age (Fig. 4). Mean duration from hatching to fledging was 47.8 d (N = 31, SD = 4.3, range = 39–61 d); however, chicks remained in the nest and were fed by their parents an average of 65.1 d after fledging (N = 14, SD = 13.4, range = 38–88 d). Three birds returned to within 10 m of their natal site 11, 21, and 24 months after leaving the island. The youngest bird observed breeding was two years and 11 months old.

Breeding success.—In 1990, a combination of severe storms during peak laying period and depredation of chicks by Great Frigatebirds (*Fregata minor*) resulted in poor reproductive success in comparison with 1991 and 1992 (Table 5). Similarly, breeding success was poor from February 1 to June 23, 1992; only three of 79 eggs laid hatched, and no chicks survived to fledging. However, after this date, nearly all eggs laid hatched and resulted in fledged chicks (Table 5). There was a difference in hatching and fledging success between study plots; both plots B and D had greater hatching success than A and C, while fledging success was lower in plot B and greater in plot D when compared to plots A and C

TABLE 5
BROWN NODDY HATCHING, FLEDGING, AND REPRODUCTIVE SUCCESS

	1982	1990	1991	1992
Total # eggs laid	222	1239	702	726
Total # eggs lost	51	644	128	161
Total # eggs hatched	171	595	574	565
Total # chicks found dead in nests	0	42	12	3
Total # fledged	62	15	263	324
Hatching success (%)[a]	77	48[b]	82[c]	78[c]
Fledging success (%)[a]	36	3[b]	46[c]	57[c]
Reproductive success (%)[a]	28	1.2	38	45

[a] Hatching success is the number of chicks hatched from the total number of eggs laid; fledging success is the number of chicks fledged from the total number of chicks hatched, and reproductive success is the number of chicks fledged from the total number of eggs laid.
[b] Lower than in other years; $\chi^2 = 313.2$ for hatching success and 430.4 for fledging success; df = 3; $P < 0.001$.
[c] Higher than in other years; $P < 0.001$.

($\chi^2 = 22.3$ and 60.4 for hatching and fledging, respectively; df = 3; $P < 0.001$).

DISCUSSION

Collectively, the Hawaiian Islands support between 89,500 and 150,000 breeding pairs of Brown Noddies. Nearly 32% of these occur in the northwestern Hawaiian Islands, with the largest population found on Nihoa Island (Harrison et al. 1983). Breeding Brown Noddies were documented by the Rothschild expedition at French Frigate Shoals as early as 1891, when thousands were observed nesting on Tern Island (Munro 1941). Wetmore observed 500 pairs nesting on Tern Island in 1923; however, they were not observed nesting on the island from 1953 to 1969 (in Amerson 1971). This period of non-nesting corresponds with its use by Coast Guard personnel as a LORAN station and the presence of cats and dogs on the island (Richardson 1954, Amerson 1971). In June 1967, an estimated 10,182 Brown Noddies were observed at French Frigate Shoals. However, the maximum number of nests recorded was 1675, occurring mainly on East and Whaleskate islands (Amerson 1971). Breeding noddies were observed again on Tern Island in 1977, shortly before the island was abandoned by the Coast Guard (M. Rauzon, pers. comm.). It is difficult to interpret whether an increase in the nesting population at French Frigate Shoals has occurred since 1891, but the population at Tern Island has expanded greatly since 1977 (Fig. 3; USFWS unpubl. data).

Time of arrival for breeding adult Brown Noddies and their occurrence

at a breeding colony vary among Pacific, Indian, and Atlantic ocean colonies (Table 6). In the Hawaiian Islands, Brown (1973) observed adults year-round on Manana Island but noted their absence during the day from December to March in 1971 and 1972. Similarly, noddies are year-round residents on Nihoa, Necker, and Laysan islands, but fewer adults are present during the day from December to March (Ely and Clapp 1973, Clapp et al. 1977, Clapp and Kridler 1977). Woodward (1972) noted that Brown Noddies are entirely absent from January to March on Kure Atoll. We observed adults on Tern Island year-round except during an El Niño event which occurred from October 1990 to March 1991, when adults abandoned the island and left fledglings still dependent on parental care to starve (Fig. 3). In contrast, Murphy (1936) stated that noddies from all of the sub-tropical South Atlantic Islands migrate from their nesting grounds between May and December. Similarly, Morris and Chardine (1992) reported that noddies were absent annually from Cayo Noroeste, Culebra, Puerto Rico from September to March. In Florida, Robertson (1964) noted that Brown Noddies departed the Dry Tortugas as early as May, and Watson (1908) reported that all birds were absent annually from these colonies by the end of September. We suggest that the variation in occurrence of Brown Noddies at Pacific and Indian Ocean breeding colonies versus those in the Atlantic may be due to a variety of factors, including food availability, ocean currents, and water temperature. However, there are no data to confirm these relationships.

In the Hawaiian Islands, the Brown Noddy's breeding season is erratic. Laying occurs from May to August on Manana Island (Brown 1973), while on Nihoa, Necker, and Laysan islands egg laying has been documented throughout the year (Ely and Clapp 1973, Clapp et al. 1977, Clapp and Kridler 1977). Woodward (1972) documented egg laying at Kure Atoll annually from April through August (Table 6). We observed that laying on Tern Island could occur throughout the year, although most eggs were laid between March and September during 1982 to 1992 (Fig. 3). Brown Noddy breeding phenology and synchrony has been explained as a response to food availability (Ashmole 1963). Morris and Chardine (1992) attributed variation in Brown Noddy breeding phenology to geographic differences in feeding regimes. ffrench (1990) stated that inclement weather on Soldado Rock, Trinidad, prolonged the breeding season so that two peaks of laying occurred in 1966, but during other years, only one peak of laying was recorded. High loss of eggs and chicks to high tides, inclement weather, and predation by Pied Crows (*Corvus albus*) on Aldabra Atoll in the Seychelles also caused variability in laying patterns (Diamond and Prys-Jones 1986). Likewise, Dorward and Ashmole (1963) attributed the double peaks of laying on Ascension Island to relaying or

TABLE 6

BREEDING PHENOLOGY OF BROWN NODDIES IN PACIFIC, ATLANTIC, AND INDIAN OCEAN COLONIES

Colony name	Latitude-longitude	Arrival of adults	Laying	Departure of adults	Source
Green Island, Kure Atoll, Hawaii	28°25′N, 178°10′W	March	Apr–Aug	January	Woodward 1972
Laysan Island, Hawaii	25°42′N, 171°44′W	Year-round	Variable	—	Ely and Clapp 1973
Tern Island, French Frigate Shoals, Hawaii	24°52′N, 166°17′W	Year-round	Variable	—[a]	This study
Dry Tortugas, Florida	24°40′N, 82°52′W	April	Apr–Jul	September	Sprunt 1948
Nihoa Island, Hawaii	23°35′N, 164°42′W	Year-round	Variable	—	Clapp et al. 1977
Necker Island, Hawaii	23°06′N, 161°58′W	Year-round	Variable	—	Clapp and Kridler 1977
Manana Island, Oahu	21°20′N, 157°40′W	Year-round	May–Aug	—	Brown 1973
Sand Island, Johnston Atoll, Pacific Ocean	16°45′N, 169°31′W	Year-round	Feb–Oct	—	Amerson and Shelton 1976
Cayo Noroeste, Culebra, Puerto Rico	18°21′N, 65°21′W	April	Apr–Jun	September	Morris and Chardine 1992
Little Tobago, Trinidad	11°18′N, 60°30′W	February	Mar–Jul	August	Morris 1984
Ascension Island, Atlantic Ocean	07°57′S, 14°22′W	November	Nov–Apr	May	Dorward and Ashmole 1963
Aldabra Atoll, Seychelles, Indian Ocean	09°24′S, 46°20′E	Year-round	Variable	—	Diamond and Prŷs-Jones 1986
Christmas Island, Indian Ocean	10°25′S, 105°42′E	Year-round	Apr–Sept	—	Gibson-Hill 1947

[a] In 1990, Brown Noddies deserted the island in October, leaving fledglings to starve, and did not return until May 1991.

to birds laying for the first time that had been prevented from nesting due to high seas. On Tern Island, Brown Noddy pairs attempted to renest as often as four times during a breeding season after losing an egg or chick. We know of no other study that has documented Brown Noddies relaying after losing their second and third clutches within the same breeding season. Ashmole (1963) observed that Sooty Terns will renest more frequently if loss of an egg occurs early rather than late in the incubation period. He also suggested that predation of Sooty Tern chicks by Ascension Frigatebirds (*Fregata aquila*) may have contributed to the breeding cycles observed on Ascension Island, where birds laying during the peak season are more likely to fledge young. The renesting efforts we observed on Tern Island could explain the multiple peaks in laying and, consequently, the variation in Brown Noddy breeding phenology. Predation on chicks by Great Frigatebirds, on eggs by Ruddy Turnstones (*Arenaria interpres*), and inclement weather resulting in nesting failure may all contribute to the multiple laying peaks we observed.

Brown Noddy eggs on Tern Island were significantly larger than those laid on Manana Island and at other Pacific and Atlantic ocean colonies (One-way ANOVA, $P < 0.05$; Table 7). Morris and Chardine (1992) stated that differences in egg sizes between Pacific and Atlantic ocean colonies were probably not due to a difference in body size. However, the body mass of 122 adults studied on Tern Island averaged larger than those on Cayo Noroeste, Culebra; Ascension Island (mistakenly reported as a Pacific Ocean colony by Morris and Chardine 1992); and Manana Island (SD = 16.7, range = 165–242 g, $F = 65.5$, df = 3, $P < 0.001$). Egg weight as a function of body weight has also been discussed by Rahn et al. (1975), Verbeek and Richardson (1982), and Pierotti and Bellrose (1986). Our data support the results of Morris and Chardine (1992) who found no differences in the measurements of a pair's first egg in comparison with subsequent eggs laid during the breeding season.

Mean incubation period did not differ for noddies nesting at Tern Island or Cayo Noroeste, Culebra, although both of these colonies had shorter incubation periods than did noddies on Manana Island (One-way ANOVA, $F = 118.6$, df = 2, $P < 0.001$; Brown 1973, Morris and Chardine 1992). Mean incubation shift lengths for noddies on Tern Island were also shorter than those observed on Manana Island (Brown 1973) and the Dry Tortugas, where Watson (1908) reported shifts occurring every two hours during the day. Finally, birds at both Tern and Manana islands switched most often during the morning and night.

Although the proportion of light- and dark-colored chicks was not different between years on Tern Island, it did differ among five colonies in the Pacific and Atlantic oceans (Table 7; $\chi^2 = 72.92$, df = 4; $P < 0.001$).

TABLE 7

ASPECTS OF BROWN NODDY BREEDING BIOLOGY COMPARED TO SOME PACIFIC, ATLANTIC, AND INDIAN OCEAN COLONIES

Colony name	Incubation length (days)			Egg dimensions[a]			Chick color[b]		
	N	Mean (range)	SD	Length (mm)	Width (mm)	Weight (g)	N	% Dark	% Light
Green Island, Kure Atoll (Woodward 1972)	76	36.1 (34–40)	?	—	—	—	265	67.0	33.0
Tern Island, FFS (this study)	70	34.8 (29–37)	2	53.4 ± 2.2 (304)	36.8 ± 1.3 (304)	37.5 ± 2.9 (253)	221	26.0	74.0
Dry Tortugas, Florida (Watson 1908)	49	35.0–36.0 ?	?	52.0 ± ? ?	35.0 ± ? ?	?	—	35.0	65.0
Manana, Oahu* (Brown 1973)	12	36.0 (35.5–37.5)	0.55	52.8 ± 2.2 (129)	36.0 ± 0.9 (129)	36.3 ± 2.5 (68)	392	51.0	27.0
Sand Island, Johnston Atoll (Amerson and Shelton 1976)	93	35.6 (30–41)	?	—	—	—	573	48.5	51.5
Cayo Noroeste,* Culebra (Morris and Chardine 1992)	37	34.5 ?	0.6	51.7 ± 1.8 (345)	35.4 ± 0.8 (345)	34.3 ± 2.2 (116)	215	44.0	56.0
Ascension Island* (Stonehouse and Stonehouse 1963)		—		52.7 ± 2.0 (113)	36.3 ± 0.8 (113)	33.5 ± 3.3 (32)	57	84.0	16.0
Christmas Island, Indian Ocean (Gibson-Hill 1951)	8	?	?	53.3 ± ? ?	36.0 ± ? ?	?	—	10.0	90.0

[a] Mean ± SD, N in parentheses.
[b] Brown (1973) placed 110 chicks in a gray category; these chicks were omitted from the analysis. N = number of chicks analyzed.
* Egg dimensions from these colonies compared to Tern Island, one-way ANOVA, $P < 0.05$ for all three measures.

While there were more light-colored chicks at Kure Atoll and Cayo Noroeste, Culebra, there were more dark-colored chicks on Ascension, Manana, and Tern islands. Because of the subjective methods used at all five colonies to classify chicks as either light or dark, some observer bias may explain the differences between colonies.

Brown Noddy chick growth rates on Tern Island were similar to those reported by Dorward and Ashmole (1963), Brown (1973), and Morris and Chardine (1992) at other Pacific and Atlantic ocean colonies. However, chicks on Tern Island fledged at a later age than those observed on Cayo Noroeste, Culebra (mean = 45.7 d, cf Morris and Chardine 1992) and Manana Island, although this difference may be the result of observer bias in determining when a chick has fledged. Gibson-Hill (1951) remarked that chicks are fed by their parents some weeks after learning to fly, and Brown (1973) observed a chick being fed more than 100 days after fledging. It seems likely that Brown Noddy chicks are attended at the colony and learn to forage during this time rather than leaving the colony with adults as is the case for Sooty Terns and Red-tailed Tropicbirds (*Phaethon rubricauda*) (Ainley et al. 1986). This is further supported by our observation of both members of a pair back at the breeding colony within 12 d after the departure of their fledglings from the island. Finally, although our data support Burger's (1980) conclusion that terns defer breeding until their third year, our study documents that birds can return to their natal site as early as 11 months after independence.

Ashmole (1963) attributed poor breeding success on Ascension Island to chick starvation. Likewise, Morris and Chardine (1992) concluded that higher breeding success at Cayo Noroeste, Puerto Rico, was the result of a reliable food source for adults. In contrast, Brown (1973) reported that on Manana Island all eggs hatched after June 11 were preyed upon by Black-Crowned Night-Herons (*Nycticorax nycticorax*), and although breeding seasonality was governed by food supply, the ultimate factor affecting fledging and success of the breeding season was predation on Brown Noddy chicks. Robertson (1964) also reported predation by Magnificent Frigatebirds (*Fregata magnificens*) on Brown Noddy chicks on the Dry Tortugas, although neither he nor Watson (1908) quantified the effect on reproductive success. In our study, Great Frigatebird predation was responsible for nearly all chick losses in 1990–1991 (Megyesi 1995). Anecdotal observations collected by USFWS personnel in previous years since 1979 confirm that Great Frigatebird predation occurs regularly on Tern Island. Although most Brown Noddy chick loss was attributed to frigatebird predation in this study, in 1992, Brown Noddies, Black Noddies (*Anous tenuirostris*), Sooty Terns, and White Terns (*Gygis alba*) experienced complete nesting failure, where incubating adults abandoned

pipped and hatching eggs and newly hatched chicks up to June 23. Following this date, Brown Noddies renested, and reproductive success was higher than had been observed in previous years of study. We suggest that this series of events in 1992 may be related to El Niño Southern Oscillation (Schreiber and Schreiber 1984; unpubl. data, USFWS).

The differences in fledging success between plots B and D are probably a result of Great Frigatebird predation. Plot B lies parallel to the runway and is more readily accessible to hunting frigatebirds. In contrast, plot D contained nests built in low growing vegetation that might have provided more cover from hunting frigatebirds. We suggest that lower reproductive success for Brown Noddies on Tern Island in comparison with other colonies is the result of inclement weather and constant predation pressure by Great Frigatebirds.

ACKNOWLEDGMENTS

We thank the numerous U.S. Fish and Wildlife Service staff and volunteers on Tern Island who helped to collect a decade of biological observations. We especially thank Ken McDermond and Ken Niethammer for their encouragement and support. We also thank Kyle Jones, Sheila Conant, and an anonymous reviewer who read an earlier draft of this manuscript.

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Wilson Bull., 108(2), 1996, pp. 335–341

DISCRIMINATION BETWEEN REGIONAL SONG FORMS IN THE NORTHERN PARULA

DANIEL J. REGELSKI[1,2] AND RALPH R. MOLDENHAUER[1]

ABSTRACT.—Distinctly different territorial (Type A) song forms characterize western and eastern populations within the breeding range of the Northern Parula (*Parula americana*). We conducted playback experiments to determine if territorial males respond differentially to the two song forms. Male response is stronger to Type A songs of their own population than to the songs of the other population (two-tailed Wilcoxon test, $P < 0.001$). The possible basis for this discrimination is discussed. *Received 3 Dec. 1993, accepted 15 Oct. 1995.*

Many oscine species exhibit geographic song variation (Thielcke 1969), and some of these species' songs vary microgeographically, with two or more small scale local dialects (Kroodsma 1981, Tomback et al. 1983, Kroodsma et al. 1984). In species such as the Mourning Warbler (*Oporornis philadelphia*), there is macrogeographical song variation, with two or more distinct and widespread regional song forms or song populations (Pitocchelli 1990).

The Northern Parula (*Parula americana*) has two primary song types, Types A and B (Moldenhauer 1992). Spectrographic analysis of Type A songs from throughout the breeding range by Moldenhauer (1992) revealed an eastern and a western song population (Fig. 1) whose songs are characterized by distinctly different terminal notes (Fig. 2). Playback experiments have shown that in species whose song varies geographically, territorial males can often distinguish between different dialects or song forms, as inferred from the intensity of response to playback (Kroodsma et al. 1984, Ritchison 1985). Usually, the response is stronger to local or familiar song forms. In the present study we conducted playback experiments with eastern and western Northern Parulas to determine if territorial males would respond differentially to eastern and western forms of the Type A song.

METHODS

Our experimental design and data analysis follow Kroodsma et. al. (1984) and Kroodsma (1989), with certain modifications. We obtained over 100 Northern Parula Type A songs from the Texas Bird Sound Library (TBSL) at Sam Houston State Univ. in Huntsville, Texas, the Cornell Library of Natural Sounds (CLNS) at Cornell Univ., and The Borror Laboratory of Bioacoustics (BLB) at The Ohio State Univ.

We used REAL TIME SPECTROGRAM software (by Engineering Design, Belmont, MA) to measure the trill portion of each song for two characteristics: trill duration (TD)

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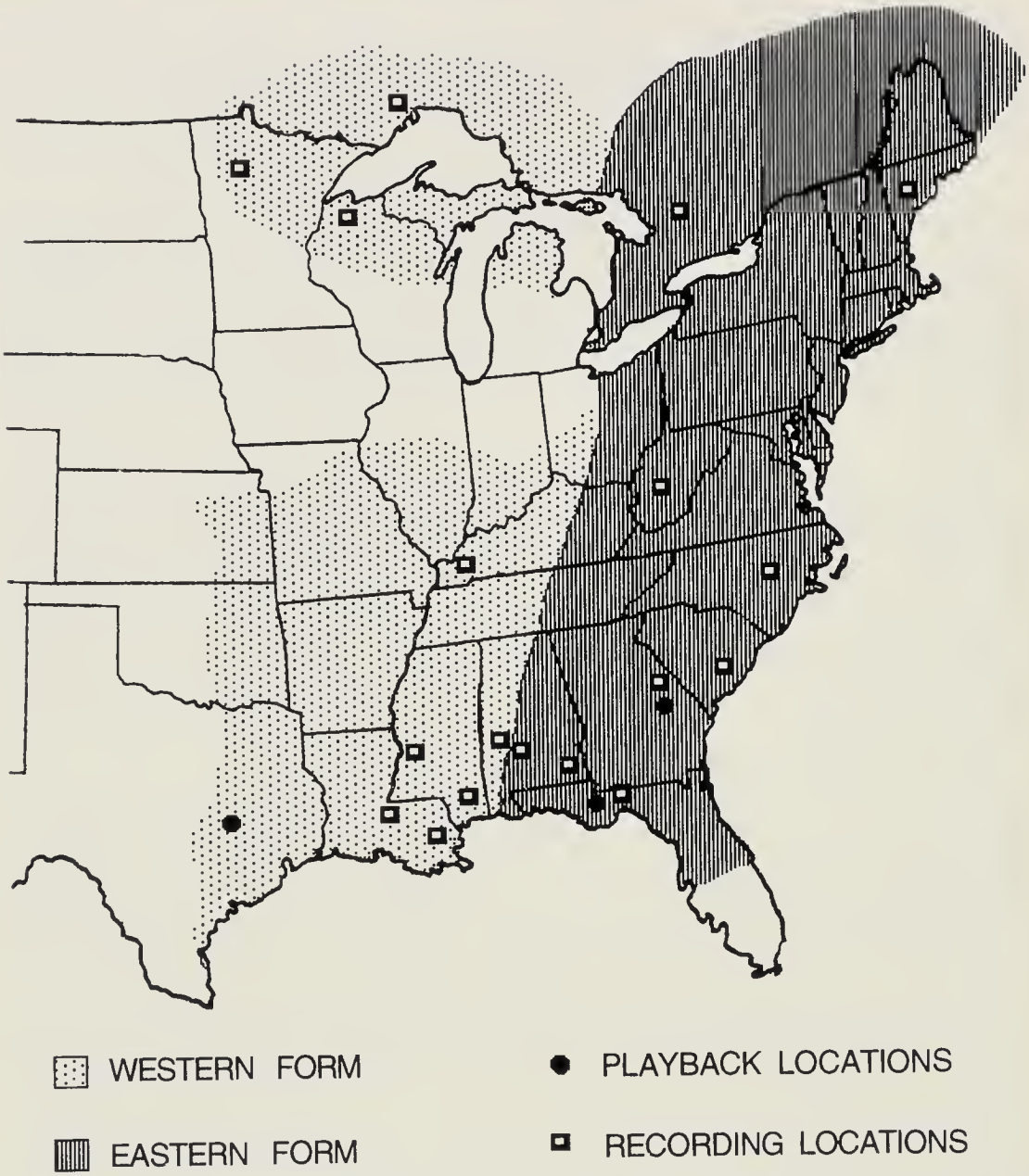

FIG. 1. Map of the distributions of the western and eastern song populations within the breeding range of the Northern Parula, as well as the recording locations for the songs used to make the playback tapes and the locations of the playback experiments.

and trill rate (TR), the number of trill syllables per second. The trill is the portion of the song preceding the last syllable or terminal note. The eastern and western populations differ significantly in the mean values for these two variables (Moldenhauer 1992). Two values were calculated for each song: TD/mean TD and TR/mean TR, using the mean values for the appropriate song population as reported by Moldenhauer (1992). The songs were arranged into pairs of one eastern and one western song that were matched as closely as possible for the values of TD/mean TD and TR/mean TR, to pair songs that were similar to one another, while taking into account the characteristics of each of the two song populations. Using this method, 12 playback tapes were made, using songs recorded at various

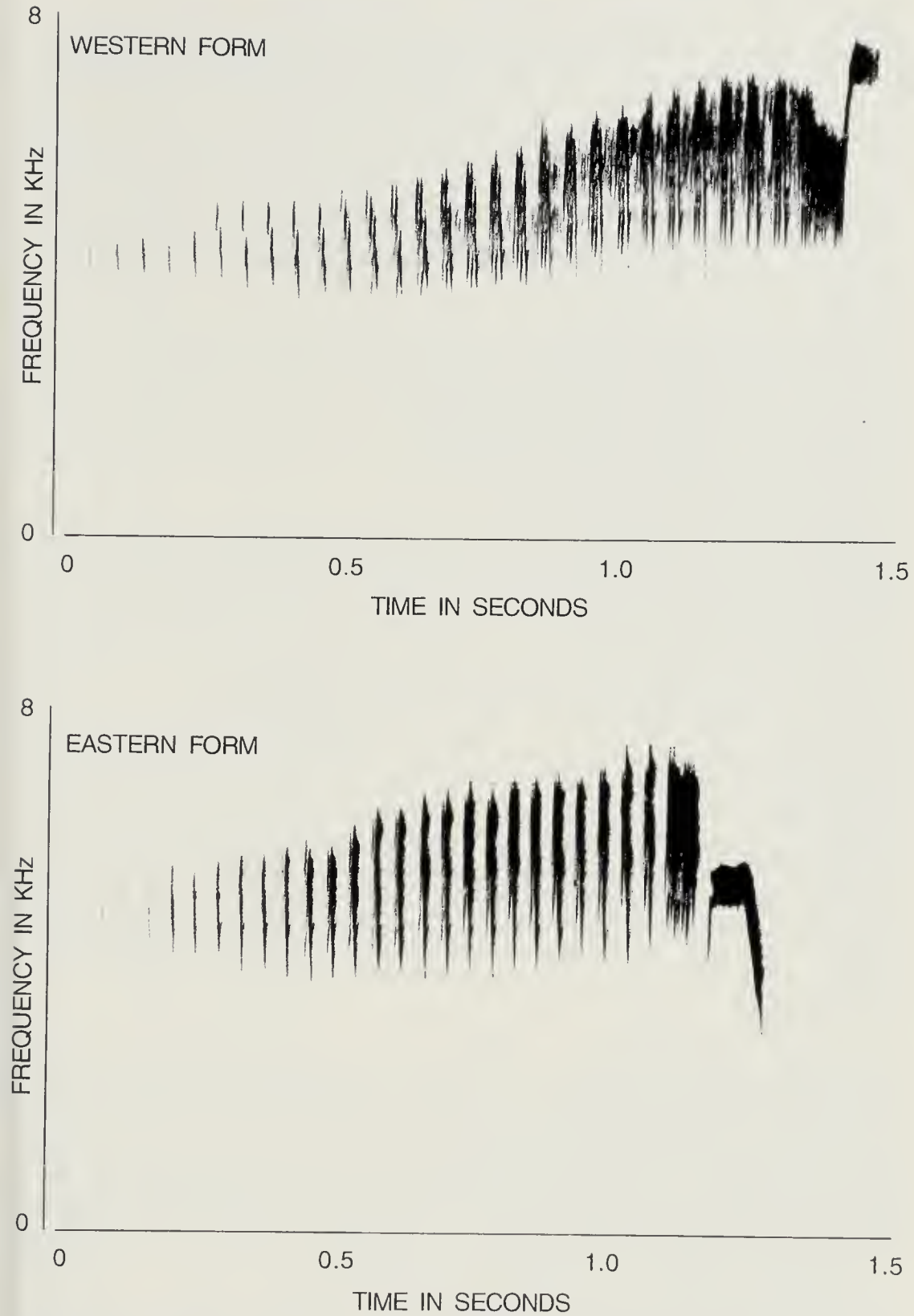

FIG. 2. Representative western and eastern forms of the Northern Parula Type A song. Notice the difference in the terminal note. These songs were used to make playback tape number 10.

dates from throughout the ranges of the two song populations (Fig. 1). Each tape consisted of 25 repetitions of one eastern song spaced 12 sec apart on the right channel, and the same treatment of one western song on the left channel. The two channels were staggered by 6 sec so that a song was broadcast from alternating speakers every 6 sec. On half the tapes an eastern song was broadcast first, on the other half, a western song was broadcast first. From 9 April to 14 May 1993, playback experiments were conducted with 12 western males near Huntsville in Walker County, Texas. From 19 to 24 May 1993, playback experiments were conducted with 12 eastern males in Liberty County, Florida, as well as Bulloch, Camden, Jenkins and Screven Counties, Georgia (Fig. 1). The same 12 tapes were used for the playbacks to both western and eastern males. This reciprocal design is discussed in Kroodsma (1989).

Songs were played on a Uher 4200 tape recorder through a pair of Radio Shack Minimus 0.8 self-amplified speakers placed 18 m apart. The playback level was set by ear to approximate a singing bird. Ribbons were placed every 2 m between the speakers, and the location of the bird during the playback period with respect to the measured 18 m was recorded every 6 s. After the first 5 min. playback period with the western song broadcast from position 0 m and the eastern song from position 18 m, the speaker cables were switched and the tape played a second time.

For the western trials, the median position of the bird during the first playback period was subtracted from the median position during the second playback period. For the eastern trials, the median position of the bird during the second playback period was subtracted from the median position during the first playback period. Positive values for difference in median positions (measured in meters) indicate a closer approach to and/or more time spent in proximity to the speaker broadcasting the bird's own song form, while negative values indicate a closer approach and/or more time spent in proximity to the speaker broadcasting the other song form. Comparing two positive values, the larger reflects a closer approach and/or more time spent in proximity to the speaker broadcasting the bird's own song form than the smaller value. Kroodsma (1989) suggests that such differences in median positions can be used as an "index of response" to the two stimuli. The greater the positive difference in median position, the stronger the response to the bird's own song type. The rationale for this method is presented by Kroodsma et. al. (1984). Therefore, we interpret closer approach to, and more time spent in proximity to a speaker broadcasting a song form, as evidenced by the difference in the bird's median position during two playback periods, as a stronger aggressive response to that song form. Hereafter, we will use the terms "stronger response" and "responded more strongly" to reflect this interpretation. Trials where the male did not approach and spend time between the speakers were not included in the analysis.

RESULTS

Ten of twelve western birds responded more strongly to their own song form, and two responded more strongly to the other song form. The bias in response is significant (two-tailed Wilcoxon test, $T_S = 8$, $P < 0.05$). Nine of twelve eastern birds responded more strongly to their own song form, and three responded more strongly to the other song form. The bias in response is significant (two-tailed Wilcoxon test, $T_S = 12$, $P < 0.025$).

To justify pooling both data sets, we compared the means of the differences in median position, a measure of the average strength of response for all 12 subjects to their own song type. These values, 4.48 m for western birds and 3.78 m for eastern birds, are not statistically different

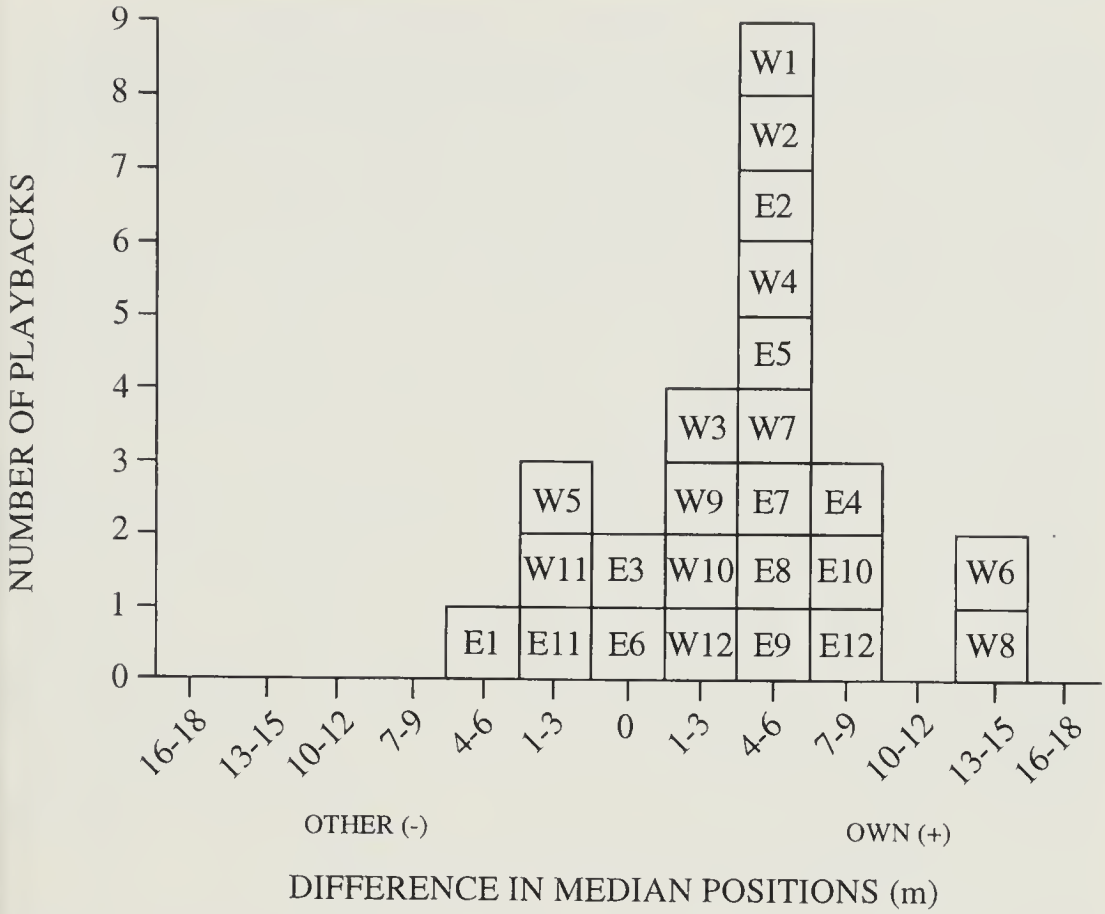

FIG. 3. Summary of all the playbacks to Northern Parulas. Each cell represents a playback session to a different male. The letter in each cell indicates whether the playback was to a (W)estern or (E)astern bird, and the number is the playback tape used. The playbacks were conducted in Texas, Florida, and Georgia. The abscissa is the difference between the median positions during the first and second playback periods. Positive values reflect a stronger response to the subject's own song form, a negative value reflects a stronger response to the other song form, and zero (0) indicates no preference. Note: for this figure, the median differences were rounded to the nearest whole number.

(two-tailed Mann-Whitney U-test $P > 0.20$). Applying Bonferroni's Inequality (Lehman 1991), the α for the test of the pooled data cannot exceed 0.049. Pooling the data gives the following results: 19 out of 24 birds responded more strongly to their own song form, and five out of 24 responded more strongly to the alternate song form (Fig. 3). The bias in response is significant (two-tailed Wilcoxon test, $T_S = 35$, $P < 0.001$). These results suggest that the birds respond more strongly to their own song form.

DISCUSSION

Territorial male Northern Parulas respond to both regional forms of the Type A song but seem to be able to discriminate between the two, as

evidenced by stronger response (closer approach, more time spent in proximity) to playback of their own song form. This resembles the pattern of response that has been observed in the Chiffchaff (*Phylloscopus collybita*), a species with macrogeographic song variation comparable to that of the Northern Parula (Thielcke and Linsenmair 1963).

In Song Sparrows (*Melospiza melodia*), the strength of response to playback of various songs increases with similarity to the subject's own song (McArthur 1986). There is also evidence that the learned association of song with aggressive behavior or territorial disputes (Payne 1986, Richards 1979) or visual stimuli (Crook 1984, Murray and Gill 1976) is involved in song form discrimination.

The two Type A song forms of the Northern Parula are relatively similar (Fig. 2), and the song probably is partially learned (Kroodsma and Baylis 1982). It is unlikely that any of the subjects had been exposed to the other song form on the breeding or wintering grounds, as the playbacks were conducted in areas of allopatry, and preliminary evidence suggests that the two song populations may have separate wintering grounds (Moldenhauer, unpubl. data). Thus, the song discrimination reported in this paper may be a result of (1) stronger response to the more structurally similar song form, (2) association of the bird's own song form with territorial disputes or aggressive interactions, (3) association of the bird's own song form with visual stimuli, such as conspecific plumage, or (4) some combination of the above. Determining how the song discrimination reported here affects gene flow in this species will require further study, especially in the area of female choice between song forms.

ACKNOWLEDGMENTS

We thank Bill and Martha Lovejoy for their hospitality; Andrew Dewees and Cecil Hallum for statistical assistance; Monte Thies for help with the figures; Donald Kroodsma, Frank B. Gill, Robert B. Payne, J. B. Dunning, Richard Bradley, and Tom C. Grubb, Jr.'s reading group and an anonymous reviewer for their comments, Frederick Weinzierl for making his property available for playback experiments, and the staff of the A. J. Brown (Parker Creek) Wastewater Treatment Plant for allowing access to Northern Parula habitat.

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Wilson Bull., 108(2), 1996, pp. 342–356

DISPERSAL AND HABITAT USE BY POST-FLEDGING JUVENILE SNOWY EGRETS AND BLACK-CROWNED NIGHT-HERONS

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Abstract.—We studied the post-fledging dispersal movements and habitat use of juvenile Snowy Egrets (*Egretta thula*) (SNEG) and Black-crowned Night-Herons (*Nycticorax nycticorax*) (BCNH) in coastal Virginia using a dye (picric acid) and radiotelemetry. Results from monitoring radiomarked birds revealed significant differences both years between species, with SNEGs dispersing more widely than BCNHs. BCNH juveniles usually remained south of Delaware, but SNEGs often moved into Delaware and southern New Jersey. The maximum dispersal distance found for a SNEG was ca 340 km north of the natal colony. Temporal patterns of movement followed logistic relationships, with rapid initial movements, but relatively few movements after about 2–3 weeks for most birds. Cumulative distances moved by juvenile SNEGs during August-September differed from 1992 to 1993. No such year difference was found for BCNHs. Compared to SNEGs, BCNHs used man-made impoundments relatively more often than natural wetlands; however no quantitative assessment of habitat preferences could be made. *Received 25 May 1995, accepted 9 Dec. 1995.*

Little is known about survival, movements, or habitat use during the post-breeding period for most North American migratory birds (Finch and Stangel 1993). Even for large, conspicuous species such as colonial waterbirds, few quantitative dispersal data have been published. Numerous anecdotal reports indicate that many terns, gulls, and wading birds move northward along the coasts and large interior rivers of the United States after the nesting season. In some regions, the movement pattern is constrained by geography, with waterbirds often following major drainages (Gill and Mewaldt 1979) regardless of the cardinal direction or following a peninsula or island archipelago (e.g., in Florida, Powell and Bjork 1990, Strong and Bancroft 1994 on Great White Herons, *Ardea herodias occidentalis*). Studies of individual species revealed some extensive northward dispersal after breeding; e.g., Black-crowned Night-Herons (*Nycticorax nycticorax*) in the eastern United States (Bartsch 1952, Byrd 1978), Little Blue Herons (*Egretta caerulea*) in Mississippi (Coffey 1943) and elsewhere in the southeast (Townsend 1931), Great White Herons in Florida (Powell and Bjork 1990), and Cattle Egrets (*Bubulcus ibis*) in Africa (Siegfried 1970).

Studies of dispersal can yield information that has both basic and ap-

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plied value. Better estimates of movement rates, habitat use, and mortality for most migrant species would assist in developing population viability analyses that are currently in demand for threatened or endangered species. Further, determining levels of site fidelity and identifying habitat types used during dispersal could have immediate management implications.

In this study, we followed movements during dispersal of juvenile Snowy Egrets (hereafter SNEGs) and Black-crowned Night-Herons (hereafter BCNHs) to address the following questions: (1) How do young birds move during the post-fledging period? Are there differences between species and years? (2) How much site fidelity do birds show during repeated observations? (3) What types of habitats do the species use during this period, and are there species differences?

STUDY AREA AND METHODS

We studied nesting ecology of two mixed-species colonies near the town of Chincoteague, Accomack County, Virginia (Fig. 1). The colonies are located in *Iva frutescens* shrubs along the margins of a saltmarsh island complex. The Causeway Colony, the largest in Virginia (Erwin et al., in press), had 230–640 SNEGs and 32–37 BCNHs in 1992–1993 in addition to large numbers of five other species. The Willis Colony had 300–390 SNEGs and 47–90 BCNHs in the two years and also included other wader species.

The habitat surrounding the colonies consisted of natural *Spartina* saltmarshes, creeks, and pannes, as well freshwater ponds and large impounded brackish marshes at the Chincoteague National Wildlife Refuge to the east.

Radio telemetry.—When nestlings were approximately two weeks old, we fixed 10 g radio transmitters to aluminum U.S. Fish & Wildlife Service bands and attached the package above the tarsometatarsal joint (see Erwin et al., in press). Radios were equipped with a mortality sensor that resulted in a 50% increase in pulse rate when the radio remained stationary for 12 h. The transmitters had a range of about 1–2 km on the ground and 5–18 km from aircraft depending on altitude and habitats. The battery life was rated at three months. We attached the radiotransmitters only to the largest chicks (presumably the A chick) in the brood to insure that we would have a reasonable sample size for monitoring post-fledging movements. We used radios only at the Causeway colony. A total of 10 and 19 radiomarked BCNHs fledged in 1992 and 1993, respectively (of totals of 10 and 20 initially marked); for SNEGs, the comparable figures were 19 and 20 (of totals of 20 initially marked both years).

In late July, when most young were fully feathered and capable of short flights (age 40–50 d), we conducted radio checks of the colonies 2–5 times weekly to estimate fledging age and to determine when to begin broader surveillance for dispersing individuals. During the initial period (1–2 weeks) after fledging, we concentrated our searches by vehicle and boat in the Chincoteague vicinity, especially on the Chincoteague National Wildlife Refuge about 6 km to the east. We began airplane surveys after all the birds had fledged. We made four flights between 12 August and 24 September in 1992 and six flights between 27 July and 2 October in 1993. We followed a regular search pattern that included the coastal areas of the DelMarVa peninsula and Delaware Bay. The basic route followed the Chesapeake shore of the peninsula from Cambridge, Maryland south to Cape Charles, Virginia, continued north along the Atlantic shore of the peninsula into Delaware Bay up to the Chesapeake

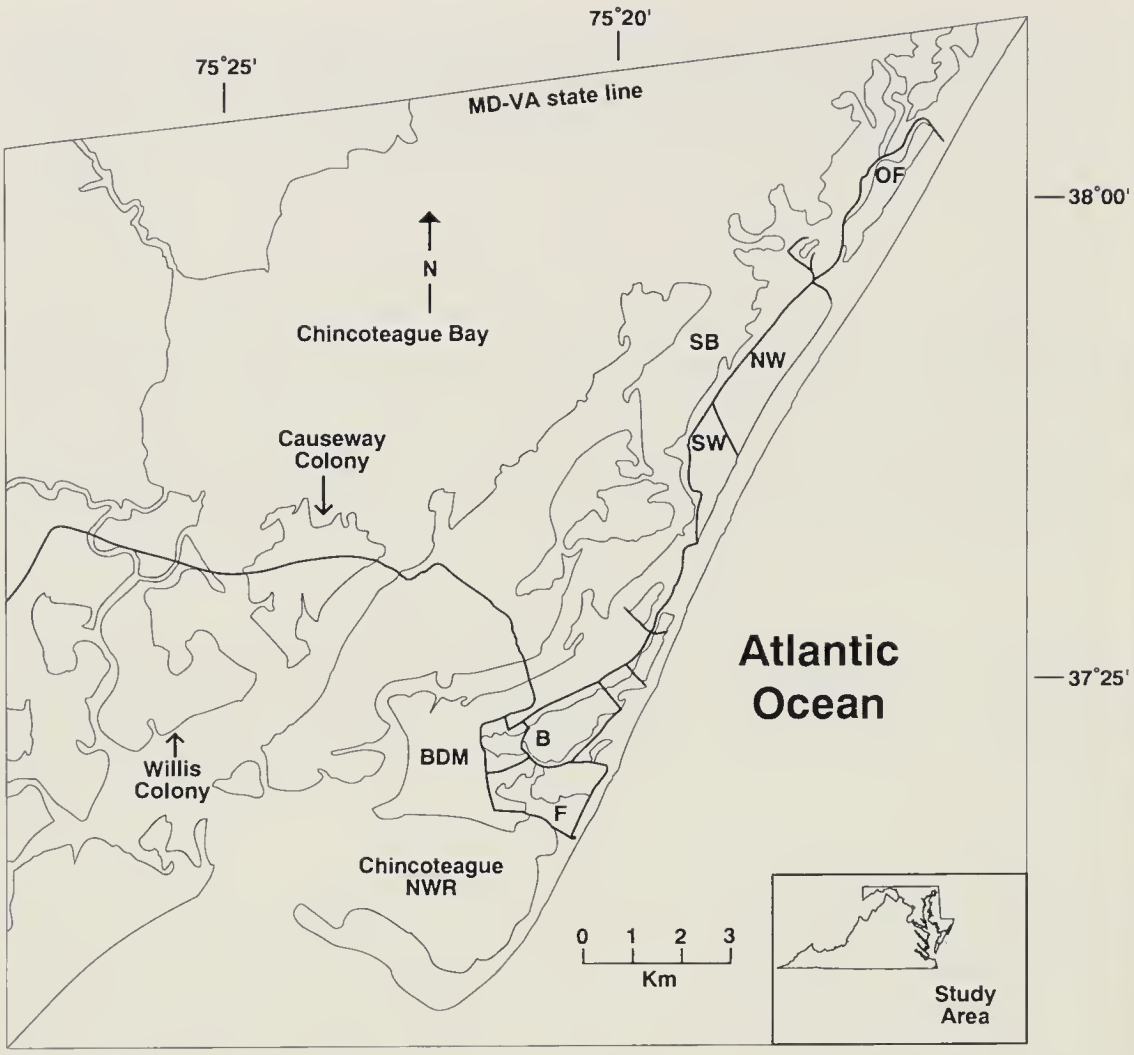

FIG. 1. Study area in coastal Virginia showing the south end of Assateague Island National Seashore, including Chincoteague National Wildlife Refuge, and two colony sites.

and Delaware (C and D) Canal, and finished along the New Jersey shoreline from Salem to Cape May. We made additional searches 1–2 times each year up the Delaware River to an area 10 km N of Philadelphia, and along the Atlantic shoreline of New Jersey from Cape May north to Manasquan. We made two flights in each year on the Chesapeake Bay side of the peninsula north of Cambridge to the C and D canal. On 1 October 1993, we made one search along the western shore of Chesapeake Bay from the lower Patuxent River south to the mouth of the James River in Virginia. Our search route and the limited range of the transmitters could have introduced some bias because we did not survey (except once) the western shore of Chesapeake Bay, nor did we effectively survey the interior of the peninsula. Funding and time precluded more exhaustive surveys. Nonetheless, species comparisons are still meaningful.

During aerial surveys, we usually maintained an altitude of 500–1000 m, scanning for birds with strut-mounted Yagi antennae. Upon detecting a signal, we circled to determine a location for the individual and identified a landmark (e.g., a named creek or impoundment) whenever possible. We recorded locations on maps, and later converted them to UTM coordinates. Because the precision of location was probably ±0.5 km, we used the center of

a large impoundment for the UTM coordinate when appropriate. All wetland locations were identified as either natural or manmade (ponds or impounded marshes).

Colormarking.—Just before most young SNEGs in the colonies fledged, we conducted a "roundup" with 7–12 participants. We held captured birds in wooden duck crates, dyed them with picric acid on the wings and back, and banded each prior to release. We marked 123 SNEGs in 1992 and 182 in 1993. After marking the birds, we continued to monitor the colonies for at least two weeks to record survival of radiomarked young and to look for any moribund or dead dyed birds. We dyed egrets in both the Causeway and Willis colonies.

To stimulate the reporting of colormarked egrets by the public and colleagues in other natural resource agencies, we sent information packages to national wildlife refuges, parks, state wildlife management areas, and state wildlife administrations from New Jersey to North Carolina. We also sent releases to a number of newspapers and magazines in the DelMarVa region. We solicited the following information: date, time, name of wetland used by the bird, wetland type, nearest town/village, band colors (if applicable), and size of associated group. Upon receiving a report, we converted map locations to UTM coordinates and, whenever possible, recorded the type of wetland used (impoundment, pond, creek).

Statistical tests.—We used the Multi-Response Permutation Procedure (MRPP) to test for large-scale differences in spatial distributions between species and years (Biondini et al. 1988). The MRPP compares the distribution of one group of points to another group using a permutation procedure (Manly 1991) and tests whether the two distributions are identical. We used this test only on the radio locations determined for birds that had left the Chincoteague vicinity. Locations reported for colormarked birds were biased because of the overrepresentation of sightings at public-access wetlands (e.g., refuges). These sightings were valuable, however, because they revealed locations that were not included in our aerial survey route.

To further investigate movements of the two species, we computed the number of relocations, total number of different wetlands used, and the cumulative distance (km) moved during the entire tracking period for each individual. Because of some locational imprecision when conducting aerial searches, we did not record a "new location" from a radiomarked bird unless it had moved ca 1–2 km from its previous location.

Because sampling intensity and duration differed between years (four aerial surveys over 6 weeks in 1992, six surveys over nine weeks in 1993), we selected a subset of radiomarked birds for standardized periods. To permit a reasonable time period for dispersal, we used data for only those individuals (N = 33 out of 48) resighted at least two times and followed at least 30 days from the time they left the colony site. After examining the raw data plots for each bird, we applied the logistic model for describing cumulative distances. The majority of individuals for which we had more than five observations revealed a sigmoidal (logistic) pattern in distances moved. We fit a separate 3-parameter logistic curve (Draper and Smith 1981) to each individual (using PROC NLIN procedure in SAS). From each of these logistic curves, we estimated the cumulative distances travelled by Day 5, 15, 30, 45, and 60. Next, to test for species and year effects, we conducted two-way ANOVAs on the cumulative distance variables for Days 5, 15, 30, 45, and 60 with Tukey tests to discern pairwise differences.

We wanted to determine gross habitat preferences for each species by comparing use of natural wetlands and manmade impoundments or ponds. However, because of our limited (coastal edge) search route and the difficulty in obtaining wetland area on the local (county) scales, we were unable to assess habitat preferences. Instead, we compared the number of individuals of each species found in the two types of habitats, and also the total number of the two wetland types used (regardless of how many individuals used them).

TABLE 1

SUMMARY OF NUMBERS OF JUVENILE SNOWY EGRETS (SNEG) AND BLACK-CROWNED NIGHT-HERONS (BCNH) RADIOMARKED IN 1992 AND 1993 AT CHINCOTEAGUE, VIRGINIA

Species	Year	No. marked that fledged	No. censored[a]	Local relocation[b,c]
SNEG	1992	19	2	10
	1993	20	6	6
	Total uncensored		31	
BCNH	1992	10	0	9
	1993	20	1	15
	Total uncensored		29	

[a] Not relocated.

[b] Relocated at least once in the Chincoteague–S. Assateague Island block (Chincoteague National Wildlife Refuge) after fledging from colony.

[c] Chi-square test for local vs nonlocal relocation by species (using uncensored totals): $\chi^2 = 6.54$, $P = 0.011$.

RESULTS

Dispersal.—From an earlier analysis, we found that juveniles fledged and left the colony when they were between 53 and 58 days old (Erwin et al., in press). Of the 29 and 39 radiomarked juveniles in 1992 and 1993, respectively, 19 and 21 individuals were recorded at least once in the wetlands within about 10 km of the nesting colony. Birds usually returned to the vicinity of the colony site at least once, or moved to the Chincoteague National Wildlife Refuge, about 6–10 km east of the colonies (Table 1). We found more juvenile BCNHs at least once in the local area (24/29 or 83%) than juvenile SNEGs (16/31 or 52%; $\chi^2 = 6.54$, $P = 0.011$). The remainder (as well as later dispersers from the Chincoteague vicinity) dispersed primarily to the north, but also west and south (Figs. 2, 3, and 4). We never located a few of the fledglings (=censored observations, Table 1); in 1992, we never located two SNEGs after fledging, whereas in 1993, we failed to locate one BCNH and six SNEGs. In 1992, SNEGs moved north into Delaware and New Jersey, whereas BCNHs were confined to Maryland and Virginia. Delaware Bay seemed to act as a partial barrier, with few birds crossing the bay into New Jersey. We received 99 reports of colormarked individual SNEGs, the majority from the Chincoteague National Wildlife Refuge. These sightings added a few new locations in 1992, with the northernmost bird reported from

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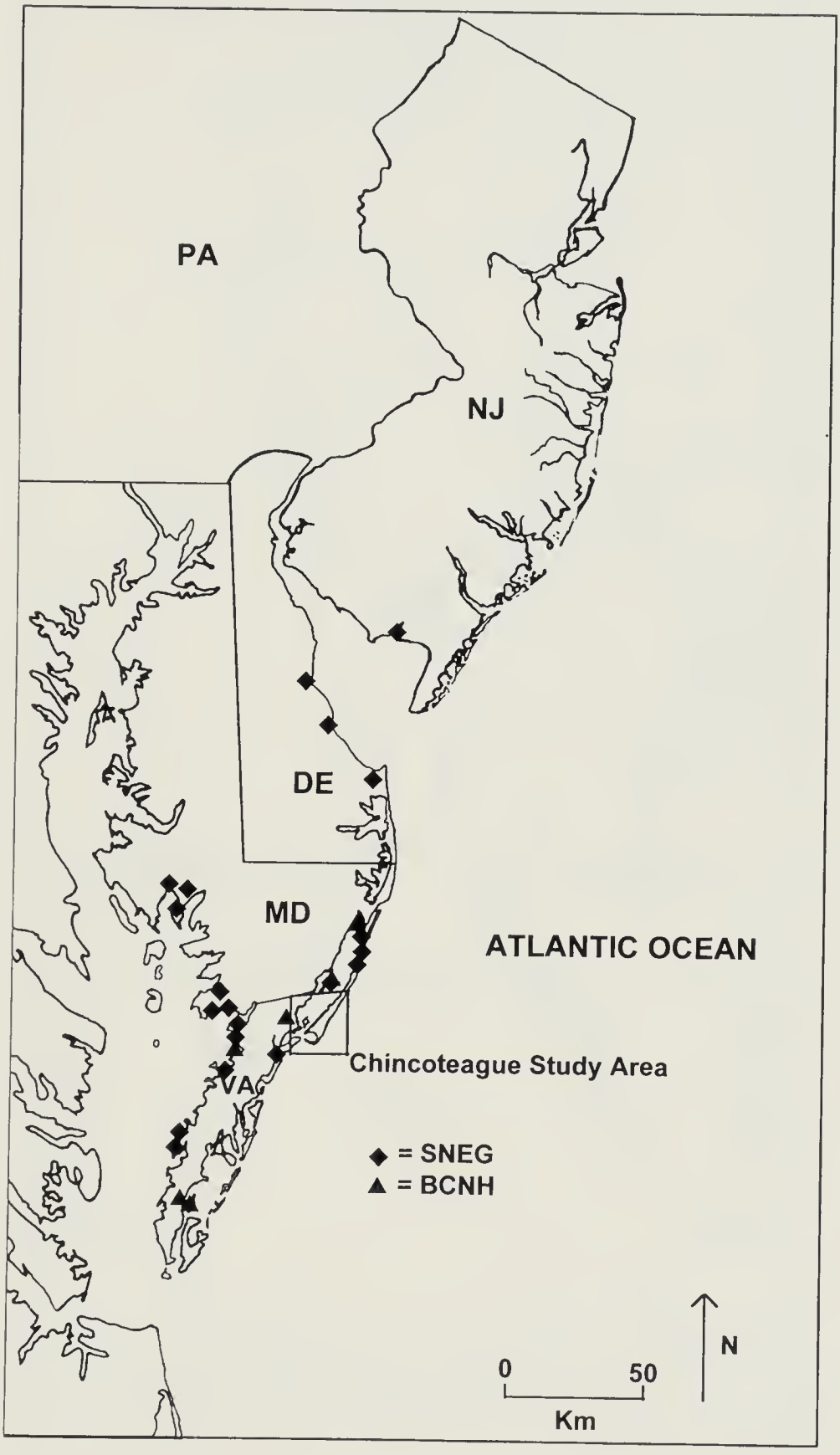
FIG. 2. Locations of radiomarked Snowy Egrets and Black-crowned Night-Herons in 1992 during August–September.


PA
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Chincoteague Study Area
◆ = SNEG
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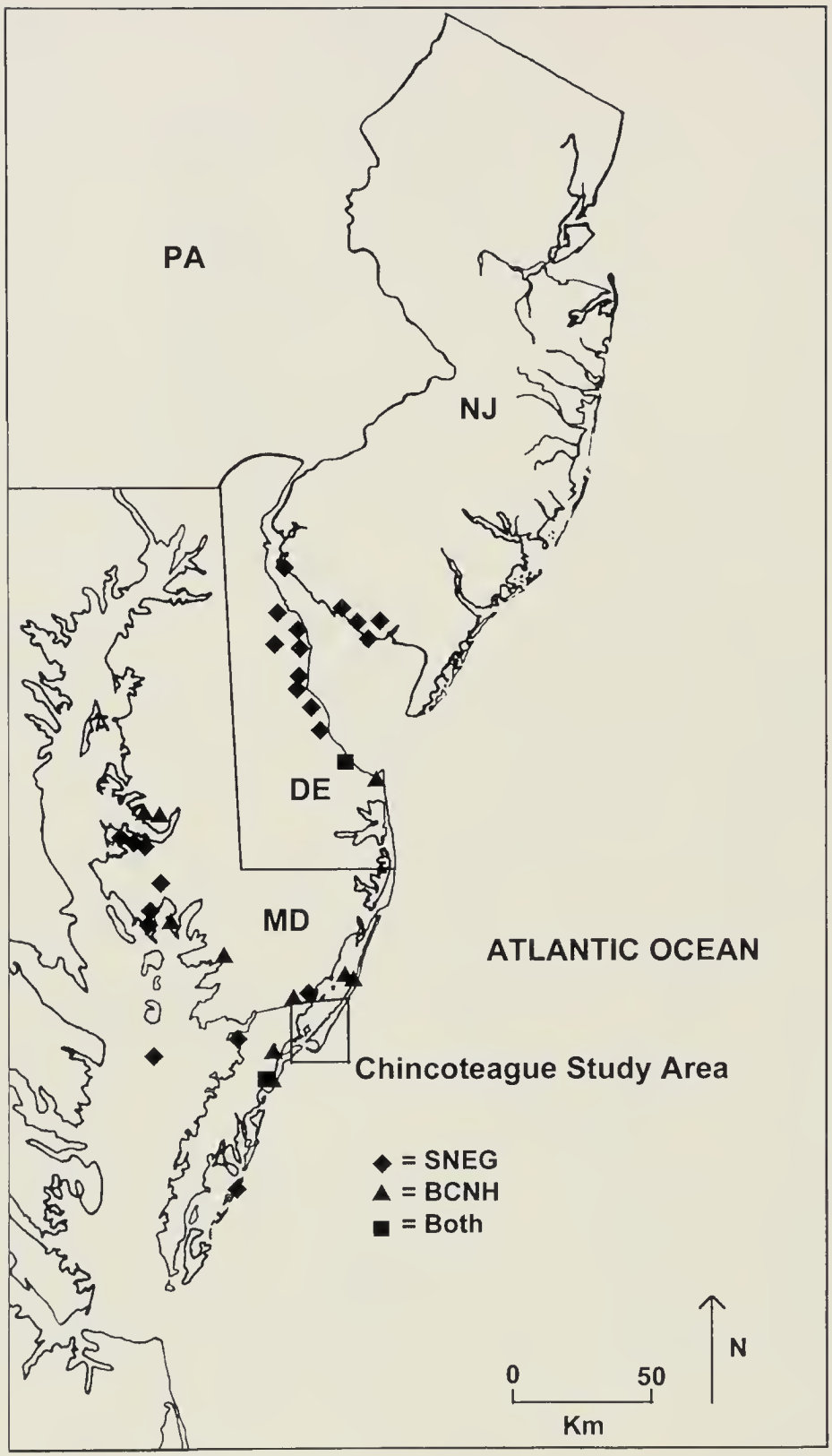

FIG. 3. Locations of radiomarked Snowy Egrets and Black-crowned Night-Herons in 1993 during late July–early October. All locations outside the Chincoteague block (nesting colony locale) are shown.

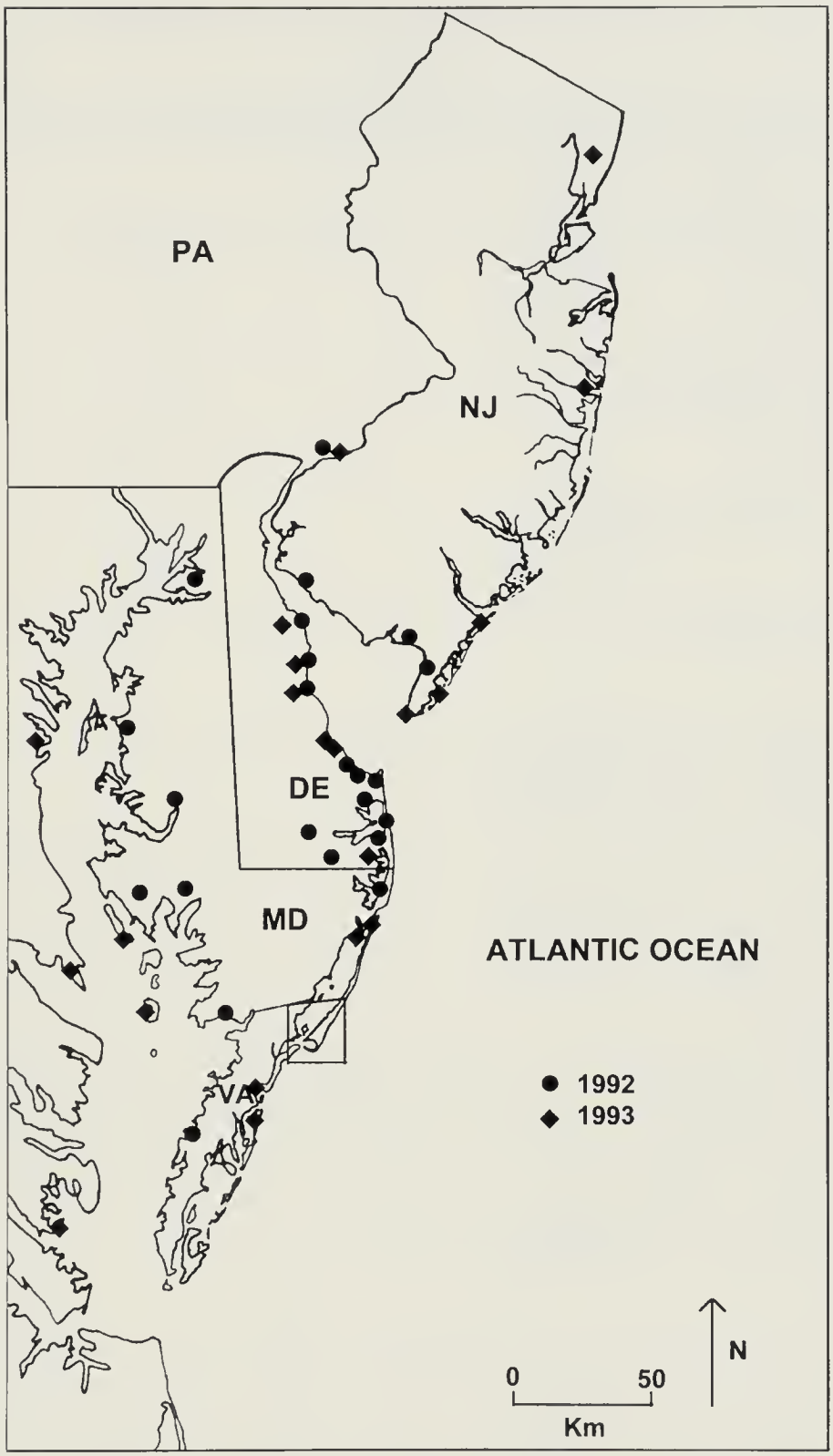

FIG. 4. Locations of dye-marked Snowy Egrets in 1992 and 1993. If two different symbols abut each other, the same location is indicated.

TABLE 2

SUMMARY OF MULTI-RESPONSE PERMUTATION PROCEDURE[a] COMPARING SPATIAL PATTERNS OF DISPERSING SNOWY EGRETS (SNEG) AND BLACK-CROWNED NIGHT-HERONS (BCNH), 1992 AND 1993

Comparison	*P* Value
Radiomarked:	
SNEG 92 vs 93	<0.001
BCNH 92 vs 93	0.02
SNEG vs BCNH (1992)	0.01
SNEG vs BCNH (1993)	<0.001
Dye-marked:	
SNEG 92 vs 93	0.18 ns
Dye vs radiomarked (SNEG):	
1992	0.002
1993	0.09 ns

[a] See Biondini et al. 1988.

the Tinicum National Wildlife Refuge south of Philadelphia about 210 km from the nesting colony (Fig. 3).

In 1993, both species generally dispersed slightly greater distances (cf Figs. 2, 3, and 4) and, the number of "lost" (censored) birds also increased. The radiomarked BCNHs moved north into Delaware, and more SNEGs were found farther north in New Jersey (Figs. 2 and 3). In 1992, no dyed SNEGs were reported west of the Chesapeake Bay, but three were seen in 1993 (Fig. 4). A total of 141 colormarked SNEGs were reported in 1993, mostly from the Chincoteague area. Also, we received a report of a dyed SNEG from far northern New Jersey in Lyndhurst, near the extensive tidal Hudson River wetlands known as the Meadowlands (Fig. 4). This location is 342 km north of the nesting colonies. In contrast, the longest distances recorded for radiomarked BCNHs were only 85 km in 1992 and 102 km in 1993.

Spatial pattern.—MRPP test results revealed significant differences ($P < 0.05$) for comparisons between years within species and between species within years for the radiomarked birds (Table 2). Dye-marked SNEGs showed no yearly difference, but their distribution was significantly different from radiomarked SNEGs in 1992 (Table 2). Although the MRPP test reveals that both species and yearly "geographic centroids" differed, the test does not indicate how the patterns differed.

Temporal pattern of dispersal.—We found a high degree of variability among individual SNEGs and BCNHs during both years of the study. A

TABLE 3

SUMMARY OF DISPERSAL MOVEMENT OF JUVENILE SNOWY EGRETS (SNEG) AND BLACK-CROWNED NIGHT-HERONS (BCNH) DURING LATE SUMMER, 1992 AND 1993

Group	Year	N[a]	Day[b]	Mean cum. distance[c] (±SD)	Mean total relocations[d]	Mean no. different locations[e]
SNEG	1992	11	5	37.2 (30.2)		
			15	50.6 (35.6)		
			30	52.5 (39.4)		
			45	52.5 (39.4)		
			60	52.5 (39.4)		
		Total			4.3	3.9
SNEG	1993	8	5	97.0 (66.7)		
			15	121.3 (61.5)		
			30	121.3 (61.5)		
			45	121.3 (61.5)		
			60	124.9 (53.9)		
		Total			6.1	4.4
BCNH	1992	6	5	17.5 (14.2)		
			15	18.4 (13.3)		
			30	21.3 (11.4)		
			45	28.1 (14.4)		
			60	44.2 (37.3)		
		Total			16.2	5.0
BCNH	1993	8	5	40.6 (47.2)		
			15	44.1 (45.1)		
			30	44.3 (44.9)		
			45	44.8 (44.4)		
			60	44.8 (44.4)		
		Total			4.3	3.0

[a] Only birds followed for >30 days, with two or more locations, were included in the analysis.

[b] To adjust for sampling intensity differences between years, values for specific numbers of days since colony departure (i.e., 5, 15, 30, 45, and 60) were predicted from the logistic curve for each bird.

[c] Means of cumulative distances moved by individuals from the colony site (origin), based on predictions from individual logistic curves.

[d] Mean number of relocations per individual during ground and air surveys in 1992 and 1993.

[e] Mean number of different wetland locations per individual during surveys. Because of locational uncertainty from aerial surveys, a "move" to a new location required an estimated 1–2 km actual relocation.

few individual herons and egrets made return trips to the Chincoteague vicinity after short dispersals, while most moved increasing distances from the colony vicinity. The general pattern was for an initial move to local wetlands near the colony site and at the Chincoteague NWR. From here, a rapid movement occurred during the next 1–2 weeks, with less movement afterward (Table 3, Fig. 5). In both years, individuals of both species moved relatively little after about 30 days, with many individuals

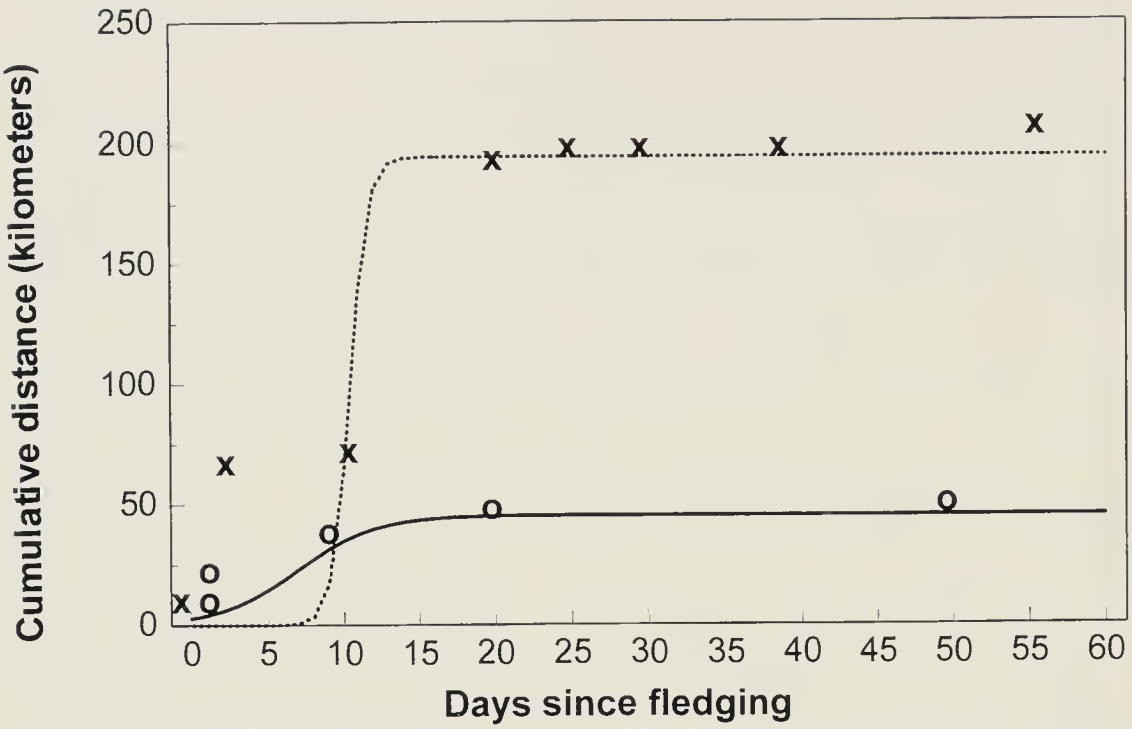

FIG. 5. Examples of cumulative distances moved over time by individual Snowy Egrets since fledging (1992 solid line, 1993 dotted line). Predicted logistic curves were generated using a three-parameter logistic equation. Symbols represent actual location distances for two individuals.

remaining in the same wetland complex (see last column in Table 3). Extreme cases in 1992 included a BCNH that spent 73 days in an impoundment at Chincoteague NWR from August 3 to October 14 (24 total relocations) and a SNEG that spent 24 days in a marsh also at Chincoteague NWR (9 relocations). In 1993, a BCNH spent 57 days (July 21 to September 15) at the same location as the previous year (13 relocations) and a SNEG spent 53 days from August 10 to October 1 at Fortesque Wildlife Management Area on the Delaware Bay shore of New Jersey.

We found several significant differences in the cumulative distances moved by dispersing birds (Table 4). For SNEGs, individuals averaged more than twice the cumulative distance in 1993 than in 1992, whereas BCNHs showed no year effect. Also, in 1993, we found a significant species effect (Tables 3 and 4).

Habitat use.—More birds of both species used natural wetlands than manmade ones (Table 5); however, habitat availability could not be assessed for the study area (see Methods). BCNHs were associated with manmade wetlands relatively more often than SNEGs in both years (Table 5). Because manmade impoundments only comprise a small fraction (15% in Delaware) of the total area of coastal estuarine emergent wetland in

TABLE 4

DIFFERENCES IN CUMULATIVE DISPERSAL DISTANCE BETWEEN SNOWY EGRETS (SNEG) AND BLACK-CROWNED NIGHT-HERONS (BCNH) IN 1992 AND 1993[a]

Comparison	Day	Difference between means (km)	Significance level ($P < 0.05$)
SNEG, 1992–1993	5	59.8	*
	15	70.7	*
	30	68.9	*
	45	68.9	*
	60	72.4	*
BCNH, 1992–1993	5	23.1	ns
	15	25.7	ns
	30	23.1	ns
	45	16.7	ns
	60	0.6	ns
1992, SNEG–BCNH	5	19.7	ns
	15	32.2	ns
	30	31.2	ns
	45	24.4	ns
	60	8.3	ns
1993, SNEG–BCNH	5	56.4	ns
	15	77.2	*
	30	77.0	*
	45	76.6	*
	60	80.1	*

[a] Two-way ANOVAs performed on cumulative distances at each predicted day, with Tukey multiple comparison test results. The corresponding one-way reparameterized ANOVAs with Tukey tests were used for interaction terms.

TABLE 5

HABITAT USE OF YOUNG RADIOMARKED BCNHS AND SNEGS IN THE DELMARVA REGION DURING THE DISPERSAL PERIOD (AUGUST–SEPTEMBER, 1992 AND 1993)

Species	Number using habitat:[a]		
	Natural	Impounded	Total
BCNH			
1992	14 (11)	11 (9)	25 (20)
1993	18 (15)	7 (10)	25 (25)
SNEG			
1992	30 (22)	4 (7)	34 (29)
1993	27 (12)	4 (6)	31 (18)

[a] First number listed is the number of locations in that habitat type with one or more individuals; in parentheses is the number of individual birds using these habitats. An individual may be counted more than once if it was found in more than one wetland.

our region, our results suggest that BCNHs may show some preference for manmade over natural wetlands.

DISCUSSION

Dispersal pattern.—The MRPP test results suggest that juvenile SNEGs and BCNHs disperse in somewhat different ways, with SNEGs more free ranging (see Figs. 4–5). The greater tendency for BCNHs to remain in the local region of their natal colony is reflected by the high frequency with which we located individual BCNHs within the Chincoteague region in both years (Table 1).

Reports of the dye-marked SNEGs indicated that our radiomarking data were probably underestimating the overall movements of birds. At least one dye-marked SNEG was found 342 km north of the natal colony (about 130 km farther than the farthest radiomarked individual and well beyond the 240 km northward extent of our aerial surveys). Reports of dye-marked SNEGs also were reported from the southwestern shore of the Chesapeake Bay in 1993, an area beyond our normal aerial search route. Perhaps the censored birds rapidly left our DelMarVa search area. However, radiotelemetry studies are often plagued by a failure to distinguish radio failures from movements beyond the survey area.

The results from our dyed egrets and those from studies in southern New Jersey (W. Crans, Rutgers Univ., unpubl. data), from which SNEGs moved into southern New England after dispersal, suggest that SNEG dispersal is greater northward than our telemetry results suggests.

Both species showed a rapid initial movement away from the natal colony area, but made relatively restricted movements thereafter, resulting in a logistic relationship for cumulative distance traveled. Such a pattern may result from local depletion of prey resources during the long nesting period in the colonies. Others have noted a similar movement pattern. Powell and Bjork (1990) found that most radiomarked juvenile Great White Herons in Florida Bay rapidly moved north from the Bay to central Florida in summer. Strong and Bancroft (1994) described a rapid (>20 km the first 10 days) northward dispersal of young White-crowned Pigeons (*Columba leucocephala*) from the Florida Keys. Immature Spanish Imperial Eagles (*Aquila adalberti*) also make long solo flights soon after leaving the natal area (Gonzalez et al. 1989).

Variable water conditions may have contributed to yearly differences in dispersal by juvenile SNEGs. In 1993, the eastern shore region of Virginia suffered from a severe drought (B. Truitt, pers. comm.). Unlike the wetter conditions in 1992, by late July and early August 1993 during the wading bird dispersal period, most of the impoundments at the Chincoteague NWR were dry. This may explain why the cumulative distances

of radiomarked SNEGs averaged more than twice as far in 1993. Snowy Egrets seem to search widely for other wading birds and often concentrate in "drawdowns" in impoundments and tidal pools (Kushlan 1978, Erwin 1983). We received a report of seven dyed SNEGs in one salthay impoundment in New Jersey in August 1993 (W. Crans, unpubl. data). BCNHs, in contrast, are more generalized in feeding habitat use (Davis 1993). Because they may use freshwater ponds and creeks as well as tidal areas, they probably do not have to move as far to find adequate food.

Habitat use.—Habitat selection during the post-breeding dispersal phase for juveniles could not be fully evaluated since we lacked quantitative estimates of wetland types for our limited survey region. The general pattern seemed to show a tendency for BCNHs to use impounded areas, including both farm ponds and large wildlife impoundments, to a greater relative extent than did SNEGs.

Data on movements of juvenile Great White Herons in central-south Florida (Powell and Bjork 1990) suggested a seasonal component to habitat selection. Early and late in the season, birds seemed to settle into human-modified habitats towards the central part of the state, whereas during the middle period, they traveled shorter distances and settled into natural marshes in the southern Everglades. Gill and Mewaldt (1979) described the dispersal patterns of SNEGs and BCNHs leaving a south San Francisco Bay heronry. Both species followed nonrandom patterns, with BCNHs following the Bay edge and tributaries, while SNEGs mostly moved <50 km to the "nearest appropriate habitats." The farthest distance travelled by a SNEG in their study was 209 km from the natal colony. Neither of these studies addressed the issue of habitat use versus availability.

For young inexperienced juveniles, a critical ecological factor may be locating a concentrated source of prey, whether it be a small sewage treatment lagoon, a large impoundment, or a natural drying freshwater slough (Kushlan 1978, Powell and Bjork 1990). Site tenacity seemed to be high for many radiomarked individuals, with an average of only 3–5 different locations per species-year group (Table 3). Variation in the amount of time specific sites were used was enormous, ranging from one to 73 days at Chincoteague NWR.

ACKNOWLEDGMENTS

We thank John Schroer and his staff at Chincoteague National Wildlife Refuge, for the field logistical support, and the many volunteers (including Jason and Lindsay Erwin and David Jachowski) who assisted. W. Link helped with statistical advice, K. Fontaine assisted in preparing the manuscript, and M. Banker and K. Boone provided graphics help. C. Blem, T. Custer, C. Henny, J. Smith, and B. Watts provided useful comments on earlier drafts of the manuscript.

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Wilson Bull., 108(2), 1996, pp. 357–368

NEST-SITE SELECTION OF RED-SHOULDERED AND RED-TAILED HAWKS IN A MANAGED FOREST

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ABSTRACT.—We compared nest-site macro- and microhabitat selection of Red-shouldered (*Buteo lineatus*) and Red-tailed hawks (*B. jamaicensis*) and examined potential relationships between habitat selection and nest success in a managed forest in central Georgia. We located 12 Red-shouldered and 10 Red-tailed hawk nests during the 1994 breeding season. Circular plots (1 km^2) were mapped around each hawk nest and 100 random points, and selected macrohabitat characteristics within the plots were measured and compared. Red-shouldered Hawk nest-site macrohabitat was characterized by significantly more bottomland hardwood habitat, less older age (>50 yr) pine habitat, and larger nest-site stands than random plots. Red-tailed Hawk nest plots contained significantly more agriculture habitat, more young (6–20 yr) pine habitat, less upland hardwood habitat, less total amount of edge, fewer number of stands, and larger average stand size than random plots. Red-shouldered Hawk nest sites (0.04 ha) had more large (>69 cm DBH) trees and lower percent total canopy cover than random points. Red-tailed Hawk nests were placed close to habitat edges and openings in the canopy, and nest sites had taller trees, larger (>69 cm) trees, and greater percent understory cover than random points. Successful Red-tailed Hawk nests were placed in shorter trees than unsuccessful nests. On the study site, large floodplain forests offering mature trees were important to breeding Red-shouldered Hawks, and mature pine forest edges near openings created by silvicultural and agricultural practices were important to breeding Red-tailed Hawks. *Received 7 April 1995, accepted 15 Nov. 1995.*

Forest management practices in Georgia often are directed towards increasing the production of pine timber. Silvicultural treatments result in forest modifications that include alterations in horizontal and vertical structural diversity, stand diversity, size class distribution, and vegetative species composition (Nelson and Titus 1988). Hardwood species are usually removed from the overstory in managed pine stands. The remaining stands of pine probably provide little habitat that is suitable for raptors (Edwards 1978). Declines in Red-shouldered Hawk (*Buteo lineatus*) populations elsewhere in its range have been attributed to alterations of nesting habitat, especially riparian habitat, and replacement by the Red-tailed Hawk (*B. jamaicensis*) which is more xeric-adapted (Stewart 1949, Henny et al. 1973).

Nest-site selection of the Red-shouldered and the Red-tailed hawk seldom has been studied at the landscape level. Few studies have described nest-site habitat selection of sympatric populations of the Red-shouldered and the Red-tailed hawk (Titus and Mosher 1981, Bednarz and Dinsmore 1982), and none have described nest-site selection for either of the two

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species in the southeastern United States. We conducted a study in a managed forest (1) to determine whether Red-shouldered and Red-tailed hawks establish nest sites in proximity to specific micro- and macrohabitat types; (2) to determine how silvicultural practices could create or modify these specific habitat types; (3) to describe potential relationships between reproductive success and nesting habitat; and (4) to determine whether habitat partitioning exists between the two species.

STUDY AREA AND METHODS

Field investigations took place at Bishop F. Grant Memorial Forest, a 5718 ha wildlife management area (WMA) owned by the Univ. of Georgia School of Forest Resources and operated in cooperation with the Georgia Dept. of Natural Resources. The WMA is located in Putnam County approximately 14.5 km north of Eatonton, GA. The property lies within the southern Piedmont physiographic province, a region of broad, gently sloping topography with occasional steep or strongly sloping terrain around the major drainage basins. A majority of the existing upland habitat types are dominated by loblolly pine (*Pinus taeda*). Present silvicultural treatments in the pine forests range from thinning and prescribed burning to clear-cutting and replanting. Bottomland hardwood habitats dominate along the property's three largest creeks (Glady Creek, Big Indian Creek, and Little River), and upland hardwood habitats exist in some areas along the drainage basins associated with these creeks. The Univ. of Georgia Agricultural Experiment Station grazes cattle on several large pastures that lie within the WMA.

We used a number of techniques to locate active Red-shouldered and Red-tailed hawk nests during the 1994 breeding season. We searched for old nests during the preceding winter months and later returned to check for signs of activity. Because taped calls of conspecific vocalizations have proven effective in locating nesting raptors (Rosenfield et al. 1988, Kimmel and Yahner 1990), Red-shouldered Hawk alarm calls were broadcast from a cassette recorder near potential nest sites. Vocalizations were played for 15-s periods distributed evenly over 5 min. Broadcasting was repeated every 10–20 min while an investigator moved through the wooded area (Mosher et al. 1990). When Red-shouldered Hawks were present, they normally responded to the vocalizations either by calling or flying towards the broadcasts. We made extensive nest searches in areas where birds responded. Because Red-tailed Hawks are relatively conspicuous visually, we located nests by searching areas where birds were seen perched or soaring. To prevent bias, nest searches also were conducted in all forested stands (trees >20 yrs) in areas where birds were not seen or heard. Stands were searched on foot by walking transects that were spaced to permit observation of most tree crowns. These searches began in late April and were continued through mid-June. Occupied nests of both species were monitored every 7–10 days and outcomes were recorded. Nests that fledged at least one young were considered successful.

Macrohabitat analysis.—We classified habitat types on a digital database developed with the geographical information system (GIS) software package ARC/INFO (Environmental Systems Research Institute 1987). Pine habitats were separated into five types based on age (numbers indicate age of forest in years): <6PINE; 6–20PINE; 21–30PINE; 31–50PINE; >50PINE. Three additional habitats types included in the analysis were bottomland hardwoods (BOTTOM), upland hardwoods (UPLAND) and agricultural land such as pastures and fields (AGR). Once nests were located and verified as occupied, they were recorded on the GIS database within the habitat types in which they occurred. To characterize available habitat, we selected 100 random points from a UTM coordinate grid using a random number

generator. Since hawks require large trees as nest substrates, only random points that fell within forested habitat greater than 20 years old were selected for analysis.

When analyzing macrohabitat preference, it is important to know the scale at which selection occurs. Sedgwick and Knopf (1992) analyzed nesting habitat within three concentric circles of increasing size using the nest site as the center. Lehmkuhl and Raphael (1993) also assessed owl habitat pattern within three concentric circles centered on foraging locations. Using a similar technique and a GIS, we mapped concentric circles of increasing size around each nest site and random point. The central circle, or mesoplot, was 1 km^2 (radius = 564 m) which was approximately equal to the smallest Red-shouldered Hawk home range (D. L. Howell, pers. comm.). We selected the smallest home range size to minimize sampling outside of territories (Sedgwick and Knopf 1992). The innermost circle (radius = 399 m), or microplot, had an area approximately half that of the home range. An outer circle (radius = 798 m), or macroplot, encompassed twice the area of the mesoplot. For comparison and because home range size of Red-tailed Hawks in the Southeast is unknown, circles of the same size were generated around Red-tailed Hawk nests.

We measured macrohabitat characteristics of nest plots and random plots with the GIS. Area of each habitat type, amount of edge (TOTEDGE), average patch size (AVGSIZE), and number of patches within circles (#STAND) were compared for each circle size. The patch size containing the plot center (STSIZE) for each nest site and random point also was tested for differences.

Microhabitat analysis.—To quantify available habitat, we used the same random points as for the macrohabitat analysis. Field locations of the UTM coordinates selected were found using a global positioning system. At the end of the nesting season (July–Aug.), we measured nest-site vegetation using a modification (Noon 1981) of the James and Shugart (1970) technique. In this study, we defined the nest site as a 0.04 ha circular plot with the nest tree as its center. Distance to water (DISTWAT), distance to a road (DISTROAD), distance to a break in the overstory canopy (DISTOP), and distance to a change in habitat type (DISTEDGE) were determined with the GIS. Except for the nest-tree-specific variables (Table 1), the sampling was the same at random points as at nest sites. A spherical densiometer (4 samples per site) was used to measure percent canopy cover and an ocular tube (20 samples per site) was used to determine percent ground cover and percent understory cover. Heights of four dominant trees in the 0.04 ha plot were determined using a clinometer and their average was used as the site canopy height. For each species, only random points that fell within the same habitat as nests were used in comparative analysis. Limiting the random sites prevented comparing nest sites to habitats where hawks were known not to nest.

Statistics.—We used Wilcoxon rank-sum tests to compare nest sites and random points, Red-shouldered and Red-tailed hawk nest sites, and successful and unsuccessful nest sites of each species. Nonparametric analyses were used because some sample sizes were small and most data were non-normally distributed. Since nonparametric statistics were used, non-normal, percentage, and count data did not require transformation (Zar 1974). All statistical analyses were performed using the Statistical Analysis System (SAS Institute Inc. 1982).

RESULTS

Macrohabitat analysis.—Because plot scale had little effect for the two species (Moorman 1995), we used mesoplot (1 km^2) values for all analyses. Ten Red-shouldered Hawk nests were located in bottomland hardwood habitat and two were found in upland hardwood ridges bordering bottomland forest. Two of these nests were located in areas where hawks previously were not seen or heard. Red-shouldered Hawk nest sites were

TABLE 1

LIST OF ADDITIONAL NEST SITE AND RANDOM POINT VARIABLES AND EXPLANATION OF THEIR MNEMONICS

Variable	Description
3–8cm(#)	Number of stems within the 0.04 ha plot with DBH between 3 and 8 cm
9–15cm(#)	Number of stems within the 0.04 ha plot with DBH between 9 and 15 cm
16–23cm(#)	Number of stems within the 0.04 ha plot with DBH between 16 and 23 cm
24–38cm(#)	Number of stems within the 0.04 ha plot with DBH between 24 and 38 cm
39–53cm(#)	Number of stems within the 0.04 ha plot with DBH between 39 and 53 cm
54–69cm(#)	Number of stems within the 0.04 ha plot with DBH between 54 and 69 cm
>69cm(#)	Number of stems within the 0.04 ha plot with DBH greater than 69 cm
BASALAREA	Total basal area per hectare
SHRUBDEN	Estimate of the number of shrubs per hectare
CANHT(m)	Average height of four dominant trees in the 0.04 ha plot
GRCOVER(%)	Percent ground cover determined with an ocular tube
CANCOVER(%)	Percent total canopy cover determined with a spherical densiometer
UNCOVER(%)	Percent understory cover determined with an ocular tube
NESTHT(m)	Height of the nest determined with a clinometer
NETREEHT(m)	Height of the nest tree determined with a clinometer
NETREEDBH(cm)	DBH of the nest tree
PERNESTHT	Percent of the nest height of the nest tree height
NEARNGHBR(m)	Distance to nearest nest of the same species

located in larger stands ($\bar{x}$ = 194.15 ha) than random points ($\bar{x}$ = 63.8 ha) (Table 2). Nest plots had significantly more BOTTOM ($\bar{x}$ = 28.43 ha) and less >50PINE ($\bar{x}$ = 16.61 ha) than random plots ($\bar{x}$ = 9.08 ha and 33.94 ha, respectively).

Eight Red-tailed Hawk nests were in >50PINE habitat, one was in 30–50PINE habitat, and one was located in a loblolly pine within UPLAND habitat. One of the ten nests was located in an area where Red-tailed Hawks previously had not been observed. Nest plots had more AGR ($\bar{x}$ = 31.71 ha) and less UPLAND ($\bar{x}$ = 16.92 ha) and 6–20PINE ($\bar{x}$ = 7.87 ha) than random plots ($\bar{x}$ = 7.49 ha, 23.79 ha, 13.79 ha, respectively). In addition, Red-tailed Hawk nest plots had less TOTEDGE, less #STAND, and a greater AVGSIZE (Table 2).

Red-shouldered and Red-tailed hawk nest-site macrohabitats were sep-

TABLE 2

MEAN ± ONE STANDARD ERROR OF MESOPLOT VARIABLES MEASURED AT RED-SHOULDERED HAWK NESTS, RED-TAILED HAWK NESTS, AND 100 RANDOM POINTS

Variable	Red-shouldered Hawk (1.0 km²)	Red-tailed Hawk (1.0 km²)	Random (1.0 km²)
STSIZE(ha)	194.15 ± 42.32[ac]	39.66 ± 11.13	63.80 ± 7.81
BOTTOM(ha)	28.43 ± 3.21[ac]	4.07 ± 2.06	9.08 ± 1.35
UPLAND(ha)	26.67 ± 3.24[c]	16.92 ± 2.50[b]	23.79 ± 0.89
AGR(ha)	4.89 ± 1.53[c]	31.71 ± 7.62[b]	7.49 ± 1.10
<6PINE(ha)	4.18 ± 2.15	8.29 ± 3.84	5.26 ± 0.87
6–20PINE(ha)	13.78 ± 3.27	7.87 ± 4.63[b]	13.79 ± 1.10
21–30PINE(ha)	2.03 ± 1.15	0.37 ± 0.36	1.59 ± 0.44
31–50PINE(ha)	3.43 ± 2.22	5.04 ± 2.91	5.07 ± 0.83
>50PINE(ha)	16.61 ± 3.18[a]	25.74 ± 5.06	33.94 ± 1.66
TOTEDGE(km)	25.00 ± 1.39[c]	20.10 ± 1.77[b]	25.40 ± 0.39
#STAND	25.58 ± 3.01	17.30 ± 2.53[b]	22.96 ± 0.57
AVGSIZE(ha)	4.46 ± 0.45	7.45 ± 1.42[b]	4.60 ± 0.14
N	12	10	100

[a] Significant differences ($P \leq 0.05$) between Red-shouldered Hawk nest plots and random plots according to Wilcoxon rank-sum tests.

[b] Significant differences ($P \leq 0.05$) between Red-tailed Hawk nest plots and random plots according to Wilcoxon rank-sum tests.

[c] Significant differences ($P \leq 0.05$) between Red-shouldered Hawk and Red-tailed Hawk nest plots according to Wilcoxon rank-sum tests.

arated by significant differences in several variables (Table 2). Red-tailed Hawk macrohabitat was characteristic of upland habitat; Red-shouldered Hawk macrohabitat represented bottomland habitat. Red-shouldered Hawk nests were located in larger stands ($\bar{x}$ = 194.15 ha) and nest plots had more BOTTOM ($\bar{x}$ = 28.43 ha), more UPLAND ($\bar{x}$ = 26.67 ha), less AGR ($\bar{x}$ = 4.89 ha), and more TOTEDGE ($\bar{x}$ = 25.0 km) than Red-tailed Hawk nest plots ($\bar{x}$ = 39.66 ha, 4.07 ha, 16.92 ha, 31.71 ha, 20.1 km, respectively).

We found no significant differences between successful and unsuccessful nesting macrohabitats for Red-shouldered or Red-tailed hawks. Four of 12 Red-shouldered Hawk nests failed to fledge at least one young. One nest was abandoned during incubation and one was damaged during a severe storm. The causes of nest failure were unknown for the other two. Five of the 10 Red-tailed Hawk nests were successful in fledging young. Causes of nest failures were not known.

Microhabitat analysis.—One Red-shouldered Hawk pair nested in a loblolly pine, but the remaining 11 pairs placed nests in deciduous trees. Four were in American sycamores (*Platanus occidentalis*), two in sweetgums (*Liquidambar styraciflua*), two in southern red oaks (*Quercus fal-*

cata), one in a water oak (*Q. nigra*), one in a green ash (*Fraxinus pennsylvanica*), and one in an eastern cottonwood (*Populus deltoides*). Red-shouldered Hawks only nested in hardwood habitat, so only random points located in hardwood habitat were used in comparative analyses. Red-shouldered Hawk nest sites had significantly more large trees (>69 cm) and lower CANCOVER than other sites within hardwood habitat (Table 3).

All Red-tailed Hawk pairs nested in loblolly pines. Nest sites were located in either pine or upland hardwood-pine habitat, so only random points located in these habitat types were used in statistical comparisons. Red-tailed Hawks built their nests significantly closer to edges and closer to openings in the canopy than random points (Table 3). Nest sites had greater UNCOVER and more understory trees (9–15 cm) than random points. Nest sites had more large trees (>69cm) and more tall trees (CANHT) than other points within potential nesting habitat.

Red-shouldered Hawk nests were placed closer to water ($\bar{x}$ = 68 m) and farther from edges ($\bar{x}$ = 57.3 m) and openings ($\bar{x}$ = 139.1 m) than Red-tailed Hawk nests ($\bar{x}$ = 355.3 m, 14.9 m, 19.6 m, respectively). Red-shouldered Hawk nest sites had greater CANCOVER and lower SHRUBDEN than Red-tailed Hawk nests (Table 3). We also compared nest-tree variables and nearest neighbor distances between the two species (Table 4). Red-tailed Hawks nested higher (NESTHT) and higher in the tree (PERNESTHT) than Red-shouldered Hawks. Nearest neighbor distances ranged from 448 m to 4195 m for Red-shouldered Hawks and from 1389 m to 2971 m for Red-tailed Hawks. Red-shouldered Hawk nearest neighbor distances generally were smaller ($\bar{x}$ = 1322 m) than those of Red-tailed Hawks ($\bar{x}$ = 1827 m), but one pair nested in a solitary location (4195 m from its nearest neighbor). When nest-site habitat variables were compared, successful Red-tailed Hawk nests were determined to be in significantly (P = 0.02) shorter trees ($\bar{x}$ = 32.0 m, N = 5) than unsuccessful ($\bar{x}$ = 37.9 m, N = 5) nests.

DISCUSSION

The effects of plot scale were minimal for both Red-tailed and Red-shouldered hawks. Degree of differences gradually decreased with increase in circle scale, but some differences existed at the largest scale. Because the size of the mesoplot circle was based on actual Red-shouldered Hawk home ranges, final results and discussions of management implications may be most appropriately based at this scale: Red-tailed Hawk home range analysis is needed for the heavily forested Southeast. Once home range size is determined, applicability of our plot sizes could

TABLE 3

MEAN ± ONE STANDARD ERROR OF MICROHABITAT VARIABLES MEASURED AT RED-SHOULDERED AND RED-TAILED HAWK NEST SITES AND THEIR CORRESPONDING RANDOM POINTS

Variable	Red-shouldered Hawk (N = 12)	Random (N = 46)	Red-tailed Hawk (N = 10)	Random (N = 59)
DISTWAT(m)	68.0 ± 21.2[c]	163.8 ± 28.4[d]	355.3 ± 64.6	260.0 ± 19.9[d]
DISTEDGE(m)	57.3 ± 16.2[c]	43.9 ± 6.1[d]	14.9 ± 2.2[b]	39.4 ± 4.6[d]
DISTOP(m)	139.1 ± 39.8[c]	104.4 ± 11.7[d]	19.6 ± 2.4[b]	98.2 ± 11.8[d]
DISTROAD(m)	274.1 ± 56.0	183.8 ± 17.2[d]	169.7 ± 23.2	117.4 ± 13.6[d]
3–8cm(#)	19.9 ± 3.4	21.4 ± 2.0	14.2 ± 4.9	19.4 ± 2.9
9–15cm(#)	9.3 ± 1.6	9.3 ± 0.7	10.3 ± 1.7[b]	6.0 ± 0.7
16–23cm(#)	4.0 ± 0.7	5.1 ± 0.4	5.6 ± 0.7	4.0 ± 0.5
24–38cm(#)	3.4 ± 0.5	4.4 ± 0.4	3.9 ± 0.9	3.7 ± 0.3
39–53cm(#)	2.7 ± 0.4	2.2 ± 0.2	2.3 ± 0.5	2.4 ± 0.2
54–69cm(#)	0.8 ± 0.2	0.8 ± 0.1	0.4 ± 0.2	0.5 ± 0.1
>69cm(#)	0.7 ± 0.2[a]	0.2 ± 0.1	0.2 ± 0.1[b]	0.0 ± 0.0
BASALAREA	37.6 ± 3.5	33.3 ± 1.8	29.0 ± 3.0	24.6 ± 1.3
SHRUBDEN	1822.9 ± 338.7[c]	3421.2 ± 452.9	5862.5 ± 1147.1	6883.5 ± 691.8
CANHT(m)	34.5 ± 2.1	33.4 ± 0.6	32.7 ± 1.0[b]	29.4 ± 0.5
GRCOVER(%)	38.0 ± 0.07	33.0 ± 0.03	44.0 ± 0.06	53.0 ± 0.03
CANCOVER(%)	87.0 ± 0.01[ac]	91.0 ± 0.00	81.0 ± 0.02	71.0 ± 0.02
UNCOVER(%)	58.0 ± 0.05	59.0 ± 0.02	51.0 ± 0.06[b]	29.0 ± 0.03

[a] Significant difference ($P \leq 0.05$) between Red-shouldered Hawk nest sites and their corresponding random sites.
[b] Significant difference ($P \leq 0.05$) between Red-tailed Hawk nest sites and their corresponding random sites.
[c] Significant difference ($P \leq 0.05$) between Red-shouldered and Red-tailed hawk nest sites.
[d] Sample size = 50.

TABLE 4

MEAN ± ONE STANDARD ERROR OF NEST-TREE VARIABLES AND NEAREST NEIGHBOR DISTANCES MEASURED AT RED-SHOULDERED AND RED-TAILED HAWK NEST SITES

Variable	Red-shouldered Hawk (N = 12)	Red-tailed Hawk (N = 10)
NESTHT(m)	21.32 ± 1.49[a]	28.22 ± 1.18
NETREEHT(m)	37.17 ± 2.72	34.97 ± 1.33
NETREEDBH(cm)	67.17 ± 7.02	53.70 ± 2.63
PERNESTHT	56.0 ± 0.02[a]	81.0 ± 0.02
NEARNGHBR(m)	1322.99 ± 317.12	1827.47 ± 193.00

[a] Significant difference ($P \leq 0.05$) between Red-shouldered and Red-tailed hawk nests according to Wilcoxon rank-sum tests.

be addressed. However, for the purpose of this study, Red-tailed Hawk nest circle mesoplot values probably sufficed for comparative analyses.

Habitat studies are often based on nests located without a random or complete search of the study site because of the time required to locate nests. Instead, raptor nests are usually located in an area where the birds previously were seen or heard. We were able to locate an additional one Red-tailed Hawk nest and two Red-shouldered Hawk nests because we searched in areas where there were no previous hawk observations. However, these nests were not in habitat types different than the other nests in our study and probably did not alter the results of our tests.

Red-shouldered Hawk nesting habitat was characterized by greater area of bottomland habitat with nests located in large stands. Both Bednarz and Dinsmore (1981, 1982), in Iowa, and Bosakowski et al. (1992), in New Jersey, determined quantitatively that bottomland and other wetlands are important habitats for breeding Red-shouldered Hawks. Stewart (1949), Henny et al. (1973), Portnoy and Dodge (1979), and Woodrey (1986) also reported riparian forests as the predominant nesting habitat. Bednarz and Dinsmore (1981) suggested a critical floodplain forest size of 250 ha, which was much larger than the 100 ha proposed by Robbins (1979). Bednarz and Dinsmore (1982) also suggested that upland habitat surrounding smaller floodplain forests may provide sufficient habitat for Red-shouldered Hawks and act as a buffer against Red-tailed Hawk encroachment. Red-tailed Hawks historically have been described as open country raptors often found in association with agriculture and forest clearings (Bent 1937). All of the Red-tailed Hawks nested at or near the edge between forested habitat and either pasture or recently clearcut habitat. We often observed pairs foraging at the edge of expansive cow pastures or from snags in relatively large (40 and 264 ha) clearcuts. Red-

tailed Hawk nests were located near these foraging sites. Therefore, nest plots had a lower amount of edge and fewer and larger stands than random plots. Bednarz and Dinsmore (1982) also reported that Red-tailed Hawks seemed to prefer larger hunting areas with less interspersion.

Because Red-shouldered Hawks were associated with bottomland habitats and Red-tailed Hawks with upland sites, differences in nest-site macrohabitat characteristics were not surprising. Red-shouldered Hawks selected large areas of hardwood habitat, and Red-tailed Hawk nesting macrohabitat had more agricultural area. Red-shouldered Hawk nest plots also contained more edge. In their comparison of Red-shouldered and Red-tailed hawk macrohabitats, Bednarz and Dinsmore (1982) also determined that edge and number of feeding areas were important to Red-shouldered Hawks, which used numerous small marshes interspersed with forest when foraging.

If the primary step in choosing a nest site is habitat type selection, then it is important to determine what cues within that habitat type are involved in final nest-site selection. Within nesting habitat, larger trees (>69 cm) and lower percent canopy cover were the structural differences between Red-shouldered Hawk nest sites and random sites. Outside of the Southeast, nesting Red-shouldered Hawks also are associated with mature forest in or near wetland habitat. Pairs nested closer to water (Titus and Mosher 1981, Bosakowski et al. 1992) and in microhabitats characterized by larger, more mature trees (Titus and Mosher 1981, Morris and Lemon 1983, Woodrey 1986) than random sites. In Ohio, Woodrey (1986) described Red-shouldered Hawk nests as having greater percent canopy cover in association with more large trees. Because our nest sites also were characterized by more large overstory trees, a lower total canopy cover may be the result of a reduced number of understory and midstory trees in nest sites.

All Red-tailed Hawk nests were in loblolly pines in either pine or upland hardwood-pine habitat. No other study has shown an exclusive use of conifers as nest trees (Bent 1937, Fitch et al. 1946, Seidensticker and Reynolds 1971, Titus and Mosher 1981). Because deciduous trees were readily available, loblolly pines may have some important structural characteristics preferred by Red-tailed Hawks. Perhaps the loblolly pine's straight growth form or open canopy provides easier access to the nest (Bednarz and Dinsmore 1982).

The large diameter trees and well-developed understory at Red-tailed Hawk nest sites are characteristic of mature pine microhabitats. Nest sites were closer to openings and edges, had a greater canopy height, and had taller trees than other sites within pine and hardwood-pine habitat. Each of these characteristics favors easy nest access. Other studies also deter-

mined that nest access was important in Red-tailed Hawk nest-site selection. Speiser and Bosakowski (1988) determined that Red-tailed Hawks nested closer to forest openings and on steeper slopes than random sites. Titus and Mosher (1981) and Bednarz and Dinsmore (1982) also found that pairs nested on steeper slopes.

Red-shouldered Hawks nested in sites with greater percent canopy cover and lower shrub density, which are both probably correlates of the habitat in which the birds nested. Floodplain forests tended to have a sparser shrub layer and a more dense canopy than upland pine habitat. By placing nests high in the nest tree near forest canopy openings, Red-tailed Hawks may have improved access from above. However, Red-shouldered Hawks placed nests low in the canopy, maybe improving access from below, where these agile flyers typically approach the nest. Nesting low in the canopy may protect Red-shouldered nestlings from insolation and adverse weather (Bednarz and Dinsmore 1982), and predation by large avian species (Morris et al. 1982, Woodrey 1986).

Each species selected mature forests offering more nest sites with larger trees when compared to available areas. Therefore, it may be important to leave some stands of older, larger trees in both pine and hardwood habitats to maintain these species. Encroachment by Red-tailed Hawks on Red-shouldered Hawk breeding territories was probably of minimal importance. In the study site, silvicultural activities were limited to upland pine habitat, and bottomland corridors were left undisturbed. The number of nesting Red-shouldered Hawks was relatively high and nest density was only slightly smaller than the highest recorded density (0.22/100 ha; Bosakowski et al. 1992). Although many intraspecific confrontations were observed for the species during the study, no interspecific competition for territory was noted. The minimum distance between a Red-shouldered and a Red-tailed hawk nest was 650 m, and the Red-shouldered Hawk nest successfully fledged young. Bednarz and Dinsmore (1982) suggested that forest clearing and development of pastures along drainage areas might shift the competitive advantage from Red-shouldered to Red-tailed hawks. Bryant (1986) also reported that selective cutting in woodlots and failure to maintain uncut buffer zones around traditional Red-shouldered Hawk nest sites may result in local extirpation of the species. We also agree that contiguous floodplain forests must be left relatively undisturbed to conserve this species. Large bottomland corridors should exclude Red-tailed Hawks because they provide poor canopy access from above. However, pine timber management on upland sites probably does not adversely affect nesting Red-shouldered Hawks and silvicultural and agricultural practices provide the edges and openings important to nesting Red-tailed Hawks.

ACKNOWLEDGMENTS

We thank D. L. Howell, J. H. Brunjes, and C. W. Eberly for continued help with field research. We also thank A. Harris and J. Gallagher for providing housing and on-site support and K. V. Miller and B. D. Shiver for their reviews of earlier manuscripts. This manuscript was improved by comments provided by J. C. Bednarz and two anonymous referees. Funding for this project was provided by the Daniel B. Warnell School of Forest Resources, Univ. of Georgia and McIntire-Stennis Proj. No. GEO-0074-MS.

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Wilson Bull., 108(2), 1996, pp. 369–371

SHORT COMMUNICATIONS

Avoidance of cabbage fields by Snow Geese.—Available evidence suggests that herbivores generally avoid sulfurous odors and volatile fatty acids (Mason et al. 1994) because such odors are associated with carnivore urine and feces (Nolte et al. 1994). Alternatively, or in addition, herbivores may avoid sulfur volatiles because they signal the bioaccumulation of toxicants such as selenium (Morris 1970) or because they indicate the presence of microbial degradation products that are toxic to vertebrates (Guildford et al. 1987).

Greylag Geese (*Anser anser*) avoid skatol (Neuhaus 1963), a (albeit nitrogenous) volatile present in the feces of predatory civet cats (*Civettictis civetta*) and in the fruits of some plants. Contrary to prevailing belief, the olfactory performance of birds in general is on a par with that of mammals (Clark and Mason 1989). Anecdotes provided by farmers suggest that geese rarely forage on winter cover crops in fields where cabbage had been planted the previous summer. A variety of sulfurous volatiles result from the decomposition of cabbage (*Brassica oleracea capitata*), including hydrogen sulfide, methyl disulfide, dimethyl disulfide, and various methyl mercaptans (Dateo et al. 1957, Self et al. 1963). We patterned the present series of observations to test the hypothesis that the odors of decaying cabbage repel Snow Geese (*Chen caerulescens*). We chose Snow Geese as our model species for three reasons. First, this bird is a strict herbivore. Second, large numbers of Snow Geese overwinter in southern New Jersey, our study area. They routinely forage on the winter cover crops planted in fields (Mason and Clark 1994). Thus it was possible to obtain a large number of fields in which cabbage had been planted the previous summer, and within which geese could possibly feed. Third, Domestic Geese (*Anser anser*) respond to plant odors (Neuhaus 1963, Wurdinger 1979), and captive Snow Geese will avoid high concentrations of Deer Away Big Game Repellent (IntAgra, Minneapolis, Minn.) (Mason, unpubl. obs.). The repellency of this commercially available product depends upon the production of sulfur odors and volatile fatty acids (Bullard et al. 1978).

Study area and methods.—We selected 16 fields near Cedarville, New Jersey, for study. All were physically similar (30–40 ha in size, adjacent to other agricultural fields on at least 3 sides) and within 5 km of Delaware Bay marsh habitat used by ≥30,000 overwintering Snow Geese (L. Widjeskog, N. J. Div. Fish and Game, pers. commun.).

Cabbage had been planted in eight of the fields during the 1994 growing season. Peppers (*Capsicum frutescens*, N = 6) or soybeans (*Glycine max*, N = 2) had been planted in the other eight fields. Conversations with farmers indicated that cabbage, peppers, and soybeans were rotated among all of the fields in multiyear cycles. During the observation period, all of the fields were planted with rye (*Secale cereale*). The maturity of the rye in all 16 fields was similar.

We paired cabbage and control fields on the basis of proximity; no member of any pair was more than 200 m apart. At the middle of each field, we established a 100-m transect parallel to the longest axis of the field and marked the ends of each transect with 0.4 m long wooden survey stakes.

Between 30 October 1994 and 20 March 1995, we visited all fields at seven-day intervals. During each visit, we walked each transect and collected all goose droppings with 0.5 m of the transect midline. We took the droppings to the laboratory and dried them in an oven at 37°C to a constant mass or for 72 h. We used these masses as an indication of goose activity (Mason et al. 1993, Mason and Clark 1994). We did not attempt to analyze the cover crop or the soil for the presence of sulfurous compounds, although sulfurous odors were readily apparent to us during our visits to cabbage fields.

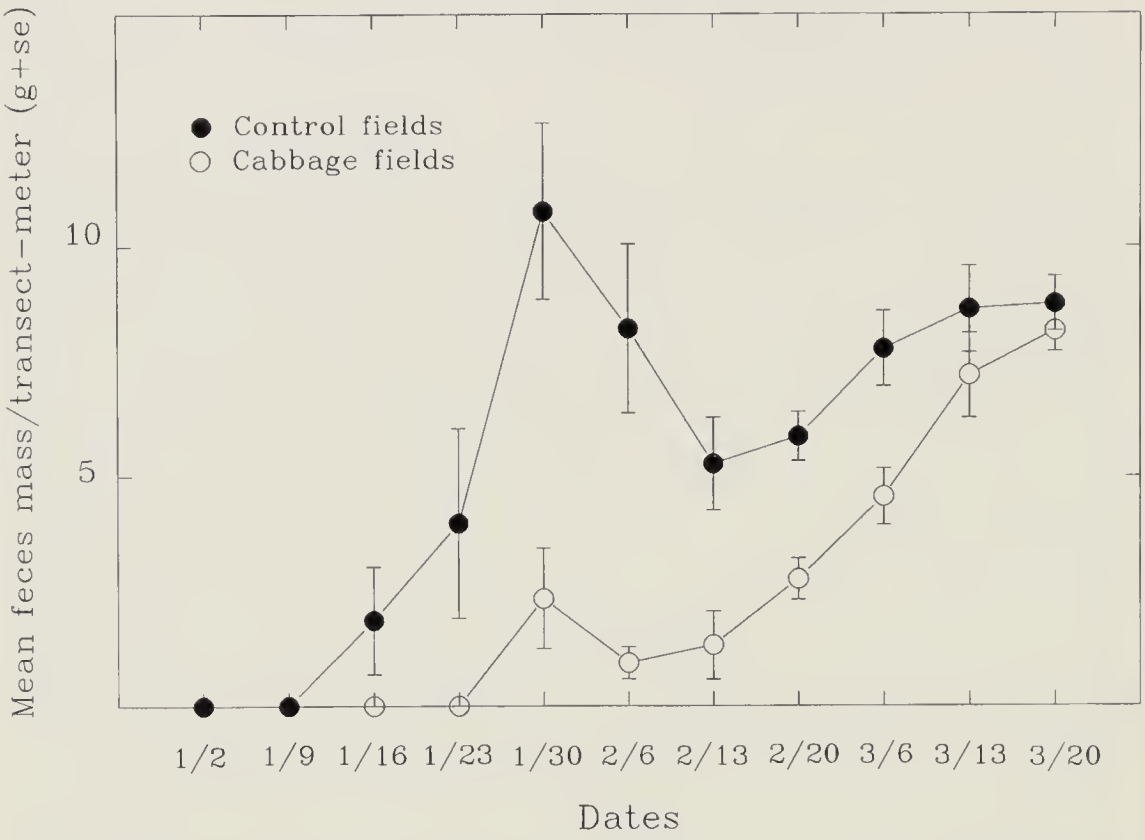

FIG. 1. Mean snow goose feces/transect meter in cabbage fields and control fields between January 2 1995 (week 1) and March 20, 1995 (week 11). Whiskers represent standard errors of the means.

We used a two-factor (sampling date, field type) repeated measures analysis of variance to evaluate the data. Subsequently, we used Tukey tests (Winer 1962:198) to isolate significant differences among means ($P < 0.05$).

Results.—No droppings were found in any field (cabbage or control) until the beginning of January. For that reason, only those data collected between 2 January 1995 and 20 March 1995 were evaluated. Overall, masses of droppings increased over time ($F = 18.3$; 10,40 df; $P < 0.0001$) and were greater in control fields than in cabbage fields ($F = 65.4$; 10,40 df; $P < 0.0002$). The significant interaction between time (dates) and field type ($F = 5.2$; 10,40 df; $P < 0.0002$) showed that differences of masses of droppings between cabbage and control fields decreased as the season progressed (Fig. 1). There were no significant differences by late March.

Discussion.—Snow Goose activity levels were significantly less in cabbage fields than in control fields. Although the data do not unambiguously address the issue of sulfur repellency, we believe that the activity difference is consistent with avoidance of the former and not preference for the latter. Sulfurous volatiles were readily apparent to us during our visits to cabbage fields throughout the study period. Similar odors were not detected in control fields. If sulfurous volatiles were important, then avoidance could reflect some characteristic of the cover crop (e.g., unpalatability acquired through the absorption and translocation of degradation products) or it could reflect an aversion to ambient (and readily detectable) volatiles in the field (Guildford et al. 1987). Regardless, our data are consistent with the notion that sulfurous volatiles may repel Snow Geese, at least within a feeding context. Perhaps sulfur

containing substances could be developed as a method for goose grazing control. Many avian species have an acute sense of smell (Davis 1973, Clark and Mason 1989, Clark et al. 1993), with variability among species similar to that observed for mammals (Fazzalari 1978). While threshold data are unavailable, there is evidence that geese are highly responsive to odorous cues (Neuhaus 1963, Wurdinger 1979, 1982).

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Wilson Bull., 108(2), 1996, pp. 372–374

Taxonomic status of the Cuban form of the Red-winged Blackbird.—The Cuban Red-winged Blackbird was described as a species, *Agelaius assimilis,* by Gundlach in Lembeye in 1850 (Ridgway 1902, Blake 1968). It was treated as a species by Ridgway (1902) who noted that it differed from the widespread Red-winged Blackbird (*A. phoeniceus*) because (1) the female plumage was uniformly black, unlike any subspecies of *A. phoeniceus* and (2) the male was smaller than almost any form of *A. phoeniceus.* Hellmayr (1937), however, treated it as a subspecies of the Red-winged Blackbird with only the following explanation: "*A. p. assimilis* is nothing but a small race of the American Red-wing with a very dark female." Subsequent authors (e.g., Barbour 1943, Bond 1956, Blake 1968, Orians 1985, Sibley and Monroe 1990) have followed Hellmayr's taxonomy, although Mayr and Short (1970) considered *assimilis* a sibling species. Recent fieldwork by Whittingham et al. (1992) has shown that the form *assimilis* differs from other populations of *A. phoeniceus* in voice and social behavior. This new evidence, combined with the similar plumage of male and female *assimilis,* leads us to conclude that this taxon is best treated at the species level. Below we summarize the evidence.

Plumage dichromatism.—Although the Red-winged Blackbird shows much geographic variation in size over its large range (e.g., Power 1969, 1970; Dickerman 1974), the basic plumage pattern of the female, brown and heavily streaked, is consistent throughout its range, except in *gubernator.* This includes populations closest to Cuba, *A. p. bryanti* of the Bahamas and *A. p. richmondi* of the tropical lowlands of Middle America. In the subspecies of the Mexican plateau, *A. p. gubernator,* female streaking is greatly reduced and limited to the throat, the remaining plumage is very dark brown (but not as black as *assimilis*). In the Californian subspecies, *A. p. californicus* and *A. p. mailliardorum,* streaking is also reduced in females and the plumage is dark brown, although not to the degree that it is in *gubernator.* Although not stated explicitly, the tendency of these populations to vary in female plumage color in the direction of *assimilis* almost certainly influenced Hellmayr's and others' decisions to regard the latter as only an end-point of the variation in female plumage of *A. phoeniceus.*

In our opinion, however, the female plumage of *assimilis* differs qualitatively from being merely an unstreaked, dark extreme in plumage variation because the plumage is uniformly coal-black, like the males and not brown, as in even the darkest forms currently treated as subspecies of *A. phoeniceus.* Furthermore, the evidence for maintaining *gubernator* as a subspecies of *A. phoeniceus* is weak (see Hardy and Dickerman 1965). Finally, in the Tricolored Blackbird (*A. tricolor*), the female has a relatively less-streaked plumage that differs from that of the male less than do male and female plumages of sympatrically breeding *A. phoeniceus.* The sexual dichromatism of *assimilis* is even less than that of *A. tricolor.* Therefore, differences in female plumage in *Agelaius* are associated with differences in taxa designated as separate species.

The plumages of nestlings and second year males also differ between *A. phoeniceus* and *A. assimilis.* In *A. assimilis,* nestling plumage is entirely dull black and some nestlings have reddish-brown lesser wing coverts (presumably males; Kirkconnell pers. obs.). In contrast, the nestling plumage of *A. phoeniceus* is entirely streaked brown (Pyle et al. 1987). Second year (SY) male *A. assimilis* are entirely black except for the orange epaulets which are mottled with black (Kirkconnell pers. obs.). In contrast, the plumage of SY males of *A. phoeniceus* is blackish with heavy white or buff streaking (Pyle et al. 1987).

Vocalizations.—Whittingham et al. (1992) compared the vocalizations of Red-winged Blackbirds in North America and Cuba. Sonographic analyses showed that male *phoeniceus* and *assimilis* songs were similar in structure; however, male *assimilis* songs were shorter

and had a greater frequency range (see Fig. 1 in Whittingham et al. 1992). In contrast, songs of female *phoeniceus* differed dramatically from those of female *assimilis*. The latter were nearly identical to male *assimilis* songs (see Fig. 1 in Whittingham et al. 1992). In contrast, *phoeniceus* females sing two song types (Beletsky 1983), each a series of individual notes that differ distinctly from songs of male *phoeniceus* or of either sex in *assimilis*. The vocal behavior of *phoeniceus* and *assimilis* also differs dramatically; *assimilis* males and females often sing their songs in a duet (Whittingham et al. 1992), whereas *phoeniceus* males and females sing only solo songs.

Mating system.—Duetting is generally associated with prolonged monogamous pair bonds (Farabaugh 1982), which suggests that the mating systems of *phoeniceus* and *assimilis* also differ. Further, studies of color-marked birds show that male and female *assimilis* are observed only in pairs whether on their breeding territories or while foraging away from their territories (Kirkconnell, pers. obs.). These observations further support the idea of a monogamous mating system in *assimilis*. In contrast, *phoeniceus* is polygynous throughout its range (reviewed in Whittingham and Robertson 1994). In some cases, males may have as many as 15 females breeding on their territory at one time (Beletsky and Orians 1990).

Validity of A. assimilis subniger.—Bangs and Zappey (1905) recognized the population on the Isle of Pines (now Isle of Youth) as *A. assimilis*. Bangs (1913) later described the population as *A. subniger* based on its coloration being very dark brown and ". . . the bill has a tendency to be rather longer and with a slightly rounded, less flattened culmen." However, the validity of these characters was questioned because the specimens Bangs examined were mostly immature (Todd 1916). Todd (1916) stated ". . . all but one of the male specimens are clearly in the immature stage. . ..the culmen is slightly flatter, it is true, in the Cuban specimens, but I believe that even this difference would disappear in a large series; at any rate, it is certainly too trifling a difference upon which to base the recognition of even a subspecies." Garrido (1970), in his revision, agreed with Todd's comments and considered the taxon *subniger* a synonym of *assimilis*.

In summary, the sexes are similar in phenotype and vocalizations in *assimilis*, whereas these characteristics differ dramatically between the sexes in *phoeniceus*. Furthermore, the plumage of nestlings and SY males as well as the mating system differs between *assimilis* and *phoeniceus*. We believe that the evidence strongly favors treatment of the taxon endemic to Cuba as a species, *Agelaius assimilis*.

Acknowledgments.—We thank J. V. Remsen Jr. and L. A. Whittingham for comments on the manuscript. (Ed. note: L. A. Whittingham helped immensely to expedite publication of this paper.)

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Wilson Bull., 108(2), 1996, pp. 374–377

Nest adoption by Monk Parakeets.—Monk Parakeets (*Myiopsitta monachus*) are unusual, being the only non-cavity nesting psittacines. Rather than using tree holes, burrows, or crevices as other parrots typically do, they build large domed nests of twigs (Forshaw 1989). Their nests often include several compartments, each with a separate entrance, and several nests may be built in the same tree or in neighboring trees. Monk Parakeets are nonmigratory and use their nests year-round for roosting as well as for breeding. Nests typically are built in trees, as well as on a variety of man-made structures (windmill towers, utility

poles, sign posts, etc.). One sub-species, *M. monachus luchsi*, builds stick nests on cliffs (Lanning 1991).

During a visit to southern Buenos Aires Province, Argentina, Humphrey and Peterson (1978) noted an association between nests of the Firewood Gatherer (*Anumbius annumbi*) and those of Monk Parakeets. They found that parakeets frequently used *Anumbius* nests as a foundation on which to build their own nests. From Humphrey and Peterson's observations, it is not clear whether or not the nests added to by parakeets had been abandoned by their original builders. In the resulting duplex nests, twigs added by the parakeets frequently engulfed the original nest, but the nest cavities were separated by a double wall, and the parakeets built and used a separate entrance tunnel.

Here, I report a similar association found during a study of Monk Parakeets in Entre Ríos Province, Argentina. A large proportion of Monk Parakeet nests were found to be remodeled nests of the Brown Cacholote (*Pseudoseisura lophotes*). The occasional adoption of Brown Cacholote nests by Monk Parakeets has been previously noted (Nores and Nores 1994); I show that adopted nests are widely used by Monk Parakeets and suggest that the association may provide a clue to understanding the evolution of the Monk Parakeet's domed nest.

Study area and methods.—During the austral spring/summers of 1993–94 and 1994–95, I studied the breeding behavior of Monk Parakeets on a portion of Estancia Santa Ana de Carpinchorí, a cattle ranch in northern Entre Ríos Province, Argentina. Parts of the ranch have been cleared, but much of it retains its native savannah woodland vegetation, which is dominated by three xerophytic trees: *Acacia caven, Prosopis affinis* and *Prosopis nigra.* I monitored the occupancy and breeding activity of all nests that were found on 1000 ha of uncleared land and that were accessible with a 7-m ladder. The locations of all nests in the study area were mapped, and for each one I measured (or estimated, in the case of very isolated nests) the distance to the nearest neighboring nest. The height to the center of each nest was measured as well. Only nests that were occupied (used either for roosting or breeding) by parakeets for at least a portion of the study are discussed here. All nests were scored as being either original Monk Parakeet nests or adopted Brown Cacholote nests that had been remodeled by parakeets. This determination was made by visual inspection of the twigs used in a nest's construction. Adopted nests are recognizable because a portion (generally the back and/or underside) of the nest comprises twigs of more variable and greater thickness than those used by parakeets (see Results).

Results and discussion.—Monk Parakeets were observed to construct nests using thorn twigs clipped from nearby *A. caven, P. affinis,* and *P. nigra* trees (usually <100 m from nest site). Twigs from other species of trees, or picked up from the ground, were used <1% of the time (JRE, unpubl. data). Parakeets consistently used the terminal ends of twigs for nest-building and occasionally used twigs stolen from nearby parakeet nests. Brown Cacholotes, on the other hand, use a variety of types and sizes of twigs (Nores and Nores 1994), resulting in a nest that, though similar in shape and size to that of the Monk Parakeet, is readily distinguishable because of the nesting materials employed in its construction. To document this difference in sizes of twigs used by the two species, I measured the mid-twig diameters of 100 randomly chosen twigs/nest from three cacholote nests and three parakeet nests. The variance and median did not vary significantly among nests within each species, so data were pooled within each species for the analyses presented here. Variance in twig diameter is much higher in cacholote nests than in nests built by Monk Parakeets (F-test: $F = 5.67$, df = 299, $P \ll 0.0001$), and twigs used by the parakeets are significantly thinner (Mann-Whitney U test: $Z = -14.55$, $P = 0.0001$, N = 600).

In the course of the two field seasons, I monitored a total of 39 accessible and occupied Monk Parakeet nests, some of which were occupied during both years. Of these 39 nests, 20 (51%) were originally cacholote nests that had been adopted and remodeled to varying

TABLE 1

NEST AND NEST-SITE CHARACTERISTICS OF MONK PARAKEETS AT ESTANCIA SANTA ANA DE CARPINCHORÍ, ENTRE RÍOS PROVINCE, ARGENTINA

Original builder	Number (% total)	Mean nest height ($\bar{x}$ ± SE)	Mean nearest neighbor dist. ($\bar{x}$ ± SE)	Number used for breeding
M. monachus	19 (48.7)	5.32 (± 0.3)	39.2 (± 16.2)	11
P. lophotes	20 (51.3)	4.5 (± 0.3)	150.8 (± 46.6)	1

extents by Monk Parakeets. This is likely to be a conservative estimate, since extensive remodeling of a cacholote nest by the parakeets could eventually engulf its foundation, leading me to score some adopted nests as originally being parakeet nests. Parakeets appeared to adopt nests that had been abandoned by their original owners and had begun to fall apart, creating an opening in the nest chamber. In their study of Brown Cacholote nesting behavior, Nores and Nores (pers. comm.) also found that monk parakeets usually moved into abandoned Brown Cacholote nests (8 of the 9 cases they observed). When remodeling cacholote nests, parakeets add twigs to the roof and around the entrance. For the six nests that I found in early stages of remodeling, parakeets had built a new entrance tunnel; however, Nores and Nores (pers. comm.) found that in eight of the nine cases of nest adoption they observed, the parakeets used the cacholote nest's original entrance. Unlike the nest association found by Humphrey and Peterson (1978) in which Monk Parakeets used *Anumbius* nests as foundations upon which to build their own nesting compartment, parakeets adopting cacholote nests always re-used the original nest's chamber.

The main site characteristics, nest height and nearest-neighbor distance and whether or not the nest was used for breeding, are summarized in Table 1. The heights of nests built by Monk Parakeets and cacholote nests adopted by parakeets did not differ significantly (Mann-Whitney U test: $Z = -1.548$, N = 39, $P = 0.12$). Adopted nests were more isolated, as reflected by their significantly longer nearest-neighbor distances (Mann-Whitney U test: $Z = -2.757$, N = 39, $P < 0.01$). Breeding attempts occurred in 12 nests, and most (92%) of these were in nests originally built by parakeets themselves. This significant preference ($\chi^2 = 12.82$, df = 1, $P < 0.005$) for breeding in non-adopted nests is probably due to the fact that these nests were more likely to be in colonies (a colony was defined as groups of nests with nearest-neighbor distances of less than 100 m). In the single case in which a breeding attempt took place in an adopted nest, the nest had been enlarged and contained two compartments, both of which were occupied.

The Monk Parakeet's willingness to adopt and remodel the nests of another species is particularly interesting in light of the fact that the Monk Parakeet is the only parrot species that builds a nest that is completely dissociated from a cavity. Nest adoption may originally have arisen in this species' ancestor as an alternative nesting strategy used by pairs unable to find or successfully compete for nesting cavities. The adoption behavior may have preceded the evolution of more complex nest-building behavior. The ability to construct a nest would then have emancipated them from a dependence on cavities or other species' nests for breeding. By giving pairs flexibility in choosing nest sites, nest-construction may in turn have facilitated the strong tendency of Monk Parakeets to breed colonially.

Acknowledgments.—During the preparation of this paper, I was supported by Princeton University and an NSF pre-doctoral fellowship. I thank the Ortíz Basualdo family and the employees of Estancia Santa Ana de Carpinchorí for their hospitality and logistical support

in the field. K. Harms assisted in the collection of field data, and P. Grant, K. Harms, and H. Horn made helpful comments on early drafts of the manuscript. I also thank D. Lanning for comments on the manuscript, as well as A. Nores and M. Nores for allowing me to include unpublished data.

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Wilson Bull., 108(2), 1996, pp. 377–378

Vermilion Flycatcher and Black Phoebe feeding on fish.—We describe our observations of two species of flycatchers, the Vermilion Flycatcher (*Pyrocephalus rubinus*) and the Black Phoebe (*Sayornis nigricans*) feeding on fish. Observations of Black Phoebes capturing fish have been noted as unusual (Bent 1942, Lawson 1975), and this is the first account of a Vermilion Flycatcher feeding on fish (Bent 1942, Terres 1980).

We made these observations at the Hassayampa River Rest Area approximately 6 km southeast of Wickenburg, Maricopa County, Arizona. On 2 Dec. 1993, we observed an adult male Vermilion Flycatcher eating a small fish. The flycatcher was first observed perched in a mesquite tree (*Prosopsis velutina*) approximately 12 m from the Hassayampa River. With binoculars we could clearly see the distal half of a fish protruding from the flycatcher's bill. It was unknown if the flycatcher captured or scavenged the fish. Vermilion Flycatchers most commonly feed by hawking for insects, but occasionally they land on the ground to feed on terrestrial invertebrates (Bent 1942, Terres 1980, Ehrlich et al. 1988, Rosenberg et al. 1991).

Andrews returned to the area on 4 Dec. 1993 and observed an adult male vermilion Flycatcher on a small mesquite tree branch 2.5 m directly over the water. After several min of observation, the flycatcher flew down, breaking the surface of the water. It then hovered just above the water for several seconds before again darting into the water. The bird hovered then darted into the water two more times. All four attempts were unsuccessful. It then returned to the same mesquite branch above the water. The depth of the water at this location was approximately 12 cm. Suspecting that the flycatcher may have been diving into the water after insects, we looked for insects or other aquatic invertebrates. No insects were observed in or over the water in the area where the flycatcher was hunting. Several large schools of longfin dace (*Agosia chrysogaster*), an abundant native fish of the family Cyprinidae, were observed at the site where the flycatcher had been hovering and diving. Attempts to photograph the flycatcher's feeding behavior were unsuccessful.

Approximately one hour after the Vermilion Flycatcher observation, Andrews saw a Black Phoebe capture a small fish, probably a longfin dace, in the same area. Although Black Phoebes feeding on small fish have been noted in the literature and reported as an unusual diet item (Bent 1942, Lawson 1975), it is noteworthy to describe here the capture and kill method used. Using binoculars, Andrews observed a Black Phoebe perched on the edge of the river looking into the water. It quickly jumped into the shallows and emerged with a small fish in its bill. The phoebe returned to the bank with the wiggling fish and forcibly threw the fish on the ground three times. When the fish ceased to move it was swallowed headfirst by the phoebe. This method of immobilizing the fish was similar to that described by Lawson (1975) who reported a Black Phoebe repeatedly striking a captured fish against a tree branch until it ceased to struggle then swallowed it, apparently headfirst. We hypothesize that the two species of flycatchers' feeding behavior was an opportunistic response to the abundance and visibility of small fish in shallow water.

Acknowledgments.—We are grateful to K. A. King for his encouragement and constructive comments on early drafts of this manuscript. We thank T. A. Gatz, for his literature search and review of the manuscript, S. Robertson for his review of the final draft, and J. Hanson for her grammatical expertise.

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Wilson Bull., 108(2), 1996, pp. 378–380

Nest-site reuse in the Western Wood-Pewee.—Reuse of the same nest site within a territory from one year to the next is well documented for birds such as colonial breeders (Shields 1984), cavity nesters (Harvey et al. 1979, Newton 1994), and species nesting on natural ledges and artificial structures (Bent 1942). In these groups, nest site reuse is promoted by the scarcity of suitable nest sites. Few non-colonial, open-nesting passerines have been documented reusing nest sites between years. Breeding studies that compare nest locations between years for this nesting guild generally report that nest sites are not reused (Hendricks 1991, Martin and Roper 1988) or are rarely reused (Nolan 1978). However, some open nesting tyrannid flycatchers, i.e., Eastern Kingbird (*Tyrannus tyrannus*) (Blancher

and Robertson 1985), Western Flycatcher (*Empidonax difficilis*), and Eastern Wood-Pewee (*Contopus virens*) (Bent 1942), regularly reuse nest sites between years. We report several instances of nest site reuse in another flycatcher, the Western Wood-Pewee (*C. sordidulus*).

During 1992–1994, we monitored the nesting dynamics of birds breeding in pinyon pine (*Pinus edulis*) - one-seed juniper (*Juniperus monosperma*) habitat in Colfax County, northeastern New Mexico. During this period, we located 46 Western Wood-Pewee nests that reached the egg-laying stage. All of these nests were in the dominant tree species, pinyon pine. In 1993, two of seven nest sites used during 1992 were reused, and in 1994, three of 15 nest sites used during 1993 were reused. One nest site was used in all three years, with the new nests constructed by adding material to the remaining portion of the previous year's nest. In other instances where the previous year's nest had fallen off the branch over the winter, the new nest was built in the same location. Because we did not band pewees on our site, individual recognition was not possible. However, we suspect that reuse involved the return of at least one individual of a pair from the previous year.

In 1993, a pewee nest which had been depredated during incubation was reused in the same season. The second clutch, initiated less than a week after the depredation event, was raised successfully, and this nest site was also reused successfully the following year. It seems unusual for birds to reuse a depredated nest or nest site (Harvey et al. 1979, Dow and Fredga 1983). A previously depredated nest might be more vulnerable to future predation than would be a new nest site, since some predators (e.g., corvids) appear to search the locations of nests that they have previously depredated, even a year later (Sonerud and Fjeld 1987).

Several explanations for the reuse of nest sites by the Western Wood-Pewee on our study area are possible, including (1) high quality nest sites may be in limited supply, despite the abundance of pinyons in the breeding habitat, (2) nest site reuse may be an extreme behavioral expression of site fidelity, and (3) pewees may benefit from time and energy savings by not searching for new nest sites or nest materials.

Acknowledgments.—We thank Scott Adair, Thomas Adams, Earl Bell, Sharon Childers, Jeff Kozma, Peter Skylstad, Boyd Trolinger, Jerrad Van't Hul, and Yan Wu for their help in observing nests. The NRA Whittington Center and V-7 Ranch provided access to their lands and logistical support for this study. Steven R. Beissinger provided helpful comments on this manuscript. This research is part of the BBIRD (Breeding Biology Research and Monitoring Database) program, which is funded by the Global Climate Change Research Program of the National Biological Service. This is BBIRD Publication # 5.

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Wilson Bull., 108(2), 1996, pp. 380–381

Nest sharing by a Lesser Scaup and a Greater Scaup.—Nest sharing has been loosely defined as two females sharing a nest, incubating their eggs together, and (perhaps) sharing in the care of the young (Terres 1982). It is a relatively uncommon phenomenon, reported infrequently in ornithological literature (see Terres 1982, for a brief review). While conducting field studies of nesting waterfowl on the islands of the North Arm of Great Slave Lake (approximately 62°30′N 115°10′W) in June 1993, we discovered a clutch of 26 scaup eggs which was being incubated by two females, one a Lesser Scaup (*Aythya affinis*) and one a Greater Scaup (*Aythya marila*). Both females flushed at close range (although not simultaneously) and were identified visually via wing stripe characteristics and size. Incubation status was determined by female behavior, egg warmth, and amount of down present at the nest.

The clutch of 26 eggs consisted of 17 "large" and nine "small" eggs, and may have been the product of more than two females. Two eggs were cracked, possibly indicating some aggressive interaction between the females. We measured a sample of eggs using vernier calipers. Three large eggs averaged 63.9 × 43.5 mm, whereas four small eggs averaged 56.8 × 42.5 mm. These measurements lie within the ranges reported for Greater and Lesser scaup, respectively (Bent 1923, Bellrose 1976, Palmer 1976). The eggs were laid in an oval-shaped depression lined with grass and were marginally concealed by a clump of grass. This arrangement provided ample room for two females to sit side by side, probably in direct contact with each other, and thereby incubate virtually the entire clutch simultaneously.

Subsequent inspection of this nest in late July revealed that it had been partially successful. Seven membranes from hatched eggs were observed. In addition, six eggs were found intact in the nest, four dead ducklings were still in their partially opened egg shells, two dead ducklings were outside their egg shells but still in the nest, and one dead duckling was found outside the nest. One egg which had been destroyed by a predator and was assumed to belong to the same nest was found nearby. The fate of the remaining five eggs could not be determined.

Skutch (1961) stated that unless the young of the two nest sharing species hatch at about the same time, and are of similar size and feeding habits, it is unlikely that the young of both species will survive. Given the ecological similarities between the two species of scaup, it is unlikely that any resulting combinations of females and ducklings that survived through departure from the nesting island would experience anything beyond the normal threats to their survival. For example, mixed age (and thus mixed size) broods and broods attended

by two or more females have been reported for both species of scaup (Bellrose 1976, Palmer 1976) and are relatively commonly observed among breeding scaup in the Great Slave Lake area (Fournier and Hines, unpubl. data).

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Wilson Bull., 108(2), 1996, pp. 381–382

Carnivory observed in the Cedar Waxwing.—On 9 Aug. 1992, I observed an adult Cedar Waxwing (*Bombycilla cedrorum*) fly to a tree branch approximately 12 m above the ground with an unidentified nestling bird in its bill. Through 7 × 35 binoculars it appeared the nestling was naked, approximately 3 cm in length and being held by the tail. It had been eviscerated, with the stomach hanging down to one side. The Cedar Waxwing paused briefly after landing, then swallowed the nestling whole in approximately three successive swallowing motions. Cedar Waxwings are frugivorous, with the exception of a relatively small proportion of invertebrate prey (Tyler 1950). To my knowledge, carnivory has not been reported for this species.

The species of the nestling was not known. It is unlikely it was a Brown-headed Cowbird (*Molothrus ater*), since cowbirds are not abundant in the area (pers. obs.), and Cedar Waxwings do not readily accept cowbird eggs (Friedmann 1963). It seems most probable the nestling was a Cedar Waxwing and was eaten either as a form of infanticide or was a dead nestling removed from the nest for hygienic reasons.

Infanticide has been reported for a variety of avian taxa (Stanback and Koenig 1992). Non-nutritional motivations for infanticide include the removal of unrelated offspring by a replacement mate and the lowering of the reproductive output of competitors (Stanback and Koenig 1992). A number of other individuals of this species were observed in the area, providing opportunity, and perhaps the motive, for infanticidal behavior. Although Cedar Waxwings may be less predisposed to cannibalism because of their largely frugivorous diet (Stanback and Koenig 1992), they are colonial nesters (Tyler 1950) which, combined with the tendency to swallow foods whole (Tyler 1950), could potentially increase their predisposition towards cannibalism (Mock 1984, Stanback and Koenig 1992). Whether or not this observation represented cannibalism or predation of another species, it certainly represents a bizarre deviation from customary Cedar Waxwing diet.

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Wilson Bull., 108(2), 1996, pp. 382–384

A case of cooperative breeding in the Hooded Warbler.—Cooperative breeding involves one or more individuals, in addition to the genetic parents, giving parental care to offspring (Stacey and Koenig 1990, Emlen 1991). In birds, this parental care may take several forms, such as feeding nestlings, nest construction, incubation, defense against predators, and territory defense (Stacey and Koenig 1990). The social organization of cooperative breeders occurs in a variety of forms including (1) nonreproductive adults helping their parents raise young, (2) "plural breeders" where more than one monogamous pair within a social group breeds simultaneously, (3) "highly gregarious" monogamous cooperative breeding groups, and (4) polyandrous or polygynandrous cooperative breeding groups (Stacey and Koenig 1990, Krebs and Davies 1991). Cooperative breeding in birds is relatively rare, existing in only 2.4% (220 of 9000) of avian species (Stacey and Koenig 1990, but see Emlen and Vehrencamp 1983). Herein, we report the first documented case of cooperative breeding in a warbler, the Hooded Warbler (*Wilsonia citrina*).

Methods.—Hooded Warblers are small, migratory songbirds that breed in selectively-logged mixed hardwood deciduous forests. We conducted this research in Crawford County, Pennsylvania (41°N, 79°W) as part of a two-year mating system study from May-August 1994 and 1995. The mating system is socially monogamous, with one male and one female occupying a single breeding territory (Stutchbury et al. 1994, Evans Ogden and Stutchbury 1994). We discovered the nest where cooperative breeding occurred on June 16, 1995. When the nestlings were five days old, a banded female, a banded male (B) and an unbanded male (U) were caught with mist nets near the nest. Unbanded adults were banded with U.S. Fish and Wildlife aluminum bands and unique color band combinations to identify individuals. Upon returning nestlings to the nest after banding them, the female and U male began chipping rapidly near the nest while the B male chipped rapidly approximately 10–15 m away. This peripheral male then flew to the nest and fed one of the nestlings.

To determine if both males were feeding nestlings, the nest was video-taped from 08:00–09:00 EDT each day for four days. Playback experiments were also conducted to determine the role of the males in territory defense. A recording of male "repeat" and "mixed" mode song patterns (Wiley et al. 1995) was used. After feeding rate observations were complete

on the fourth day, three playback experiments of a 10-min. duration were conducted in mid-morning in the center of the territory. A model of a male Hooded Warbler was placed beside the playback speaker. Playbacks were conducted at approximately 30-min. intervals. Repeating the playback experiment confirmed that the same male was responding each time.

Results.—Mean feeding rates (±SE) (N = 4 h) for the female was 7.4 ± 3.0 trips/h. Mean feeding rates for the B and U males were 9.6 ± 1.6 trips/h and 1.1 ± 0.2 trips/h respectively. The feeding rate for the B male was significantly higher (unpaired *t*-test, $t = 5.29$, df = 6, $P = 0.002$) than that of the U male. Feeding rates did not differ significantly between either the female and the B male (*t*-test, $t = -0.65$, df = 6, $P = 0.54$) or the U male (*t*-test, $t = 2.12$, df = 6, $P = 0.08$).

The degree of aggressive behavior during playbacks varied between the two males. Both males chipped rapidly and countersang within one minute of the start of the playback. However, only the B male circled repeatedly around the model (at a radius of 10–15 m), changed its perch frequently and flew within 5 m of the model twice. The U male stayed about 20–25 m away. Neither male physically attacked the model. Each time I approached the nest, all three adults flew to the nest in defense.

Discussion.—Previously in this study area, feeding behavior to nestlings has been observed for 5–6 h/nest for about 60 nests, with no prior instances of cooperative breeding (Evans Ogden and Stutchbury 1994, Neudorf, unpubl. data). Therefore, cooperative breeding is rare (1/60 or 1.5%) in Hooded Warblers. The "auxillary" male (U) could have shared paternity with the "dominant" male (B) because about 40% of female Hooded Warblers produce extra-pair young from fertilizations with neighboring males (Stutchbury et al. 1994). High levels of extra-pair matings could increase the likelihood of cooperative breeding, just as it may favor adoption of fledglings in this species (Stutchbury and Evans Ogden, unpubl. data). In 1994, the auxillary male was pair-bonded with this same female on a nearby territory, but was genetically unrelated to his offspring that year (Tarof, Stutchbury and Piper, unpubl. data). This cuckoldry, along with subsequent mate-switching the following year by the female, may be explained by the relative low quality of this auxillary male. Why the dominant male permits an ASY (after-second year) auxillary male to help raise offspring is a question that has perplexed researchers since cooperative breeding was first reported (Skutch 1935), particularly with a territorial species such as Hooded Warblers. Although males were never seen at the nest together, no overt aggression was observed. We expect that cooperative breeding may be widespread in warblers, although it likely occurs at very low frequencies within a species.

Acknowledgments.—Diane Neudorf and Joan Howlett provided advice and pertinent comments on the manuscript. We appreciate the assistance of Margaret Tarof, Diane Neudorf, Lesley Evans Ogden, and Trevor Pitcher with fieldwork. A Natural Sciences and Engineering Research Council of Canada scholarship to S.A.T. supported this research.

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Wilson Bull., 108(2), 1996, pp. 385–394

ORNITHOLOGICAL LITERATURE

Edited by William E. Davis, Jr.

A birder's guide to Arkansas. By Mel White. American Birding Association, Inc., Colorado Springs, Colorado. 1995:259 pp., 53 maps, 20 black-and-white photographs, 16 line drawings. $16.95 (soft wrap-around cover).—This is the seventh in the series of the American Birding Association's birdfinding guide series, which is a revision and extension of the Lane series which served birders well for many years. Like the other six guides published so far, this book is well-written, well-edited, and well-designed and a must for anyone interested in birds visiting an area covered by one of the series. The book is sturdy, printed on heavy paper with a wire-o binding and a wrap-around cover which serves to protect the book and/or serve as a book mark. Its roughly 15 by 21.5 cm size is small enough to fit into a car's glove box and some jacket pockets. It is designed to be used.

An introductory chapter has sections on the physiography of the state, the birding calendar, and historical and ecological notes. The book is written with humor, and the section entitled "Weather and other pests," which provides useful information on ticks, chiggers, mosquitos, poisonous snakes, etc., concludes with "Try not to walk off any cliffs." The major portion of the text describes 59 birding sites clustered into five geographic regions bounded by county lines. Each regional cluster of sites has an introduction and map of site locations, followed by detailed descriptions, including a map, of each site. The site maps are clear and readable, and descriptions of directions are given to a tenth of a mile—an excellent feature. The usual list of useful telephone numbers for the local birding "hotline," travel information, etc., are supplemented by the numbers to call for information for any of the sites in state or federal parks or preserves. Following the site guide chapters are sections on "specialty birds" and bar graphs for each species giving status (e.g., "hard to miss," "lucky to find") throughout the year. Additional appendices list "seldom-seen" and "accidental" birds, and lists of Arkansas mammals, amphibians, reptiles, and butterflies.

I cannot imagine anyone interested in birds visiting Arkansas without taking a copy of this book along.—William E. Davis, Jr.

Stories I like to tell: an autobiography. By H. Elliott McClure. Privately printed, Camarillo, California. 1995:373 pp., 110 black-and-white photograph figures. Available in paperback for $14 (S&H incl.) from H. Elliott McClure, 69 E. Loop, Camarillo, California 93010-2327.—This is the story of an entomologist turned ornithologist and naturalist who began his professional career as a wildlife biologist studying doves in the mid-west and ended it nearly 35 years later with involvement in an international bird-banding scheme in Asia. This very personal narrative includes recollections of youthful adventures from dodging streetcars with his bicycle to an awe-inspiring viewing of a local doctor's butterfly collection. The pages are full of interesting anecdotes, including many which are bird related. Twenty-five years were spend in Asia, beginning with an encephalitis study in Japan, and many adventures describe exotic birds and places. There are chapters on hornbills and bulbuls and lots of birdwatching adventures in, for example, Australia, the Philippines, Thailand, and Malaya. A lot of historical information on M.A.P.S. (Migratory Animals Pathological Survey) Asian project is woven into the latter part of the book. Several hundred photographs (usually several per figure) present a photographic collage of everything from family photos to scorpions and hornbills.

Despite the minor annoyance of the many typos, occasional grammatical collapses, lack

of an index, and a table of contents with no page numbers, I found this a delightful book full of the fun and adventures of an interesting ornithological career. The narrative is engaging, and there was enough about birds, conservation, and natural history to satisfy my ornithological cravings.—William E. Davis, Jr.

The hornbills. By Alan Kemp, illustrated by Martin Woodcock. Oxford University Press, New York. 1995: 302 pp., 14 color plates, black-and-white line drawings, 53 range maps, 7 tables, glossary. $60.—The hornbills, (Order Bucerotiformes *sensu* Sibley and Monroe. 1990. "Distribution and Taxonomy of Birds of the World." Yale Univ. Press, New Haven, Connecticut) are separated by Kemp into two families, including one genus and two species of very large (to 4000 g) ground hornbills (Bucorvidae) and 52 species and eight genera of medium to large (83–3300 g) true hornbills (Bucerotidae). The taxonomy of hornbills seems to be in a state of flux, and there are some taxonomic changes included in this book—primarily the elevation of subspecies to species level and the inclusion of some new common names. For example, Sibley and Monroe (1990) refer to *Tockus albicristatus* as the White-crested Hornbill, a translation of the specific name, whereas Kemp refers to it as the Long-tailed Hornbill. Kemp apparently used Long-tailed Hornbill to reduce confusion with the White-crowned Hornbill (*Aceros comatus*) which has also at times been called the White-crested Hornbill.

The ground hornbills are found only on the savannas of Africa; the true hornbills are forest birds of Africa, south and east Asia, and many of the islands of the Indian Ocean. Most of the hornbills have a large bill with a casque which has suggested functions ranging from sex and age recognition to sound reception, to use in foraging, nest maintenance, or territorial defense. In a dramatic introduction, territorial male Great Helmeted Hornbills (*Buceros vigil*) rivals are described as meeting in a manner analogous to the behavior of rams—by flying at one another and butting heads in mid-air! Unfortunately, it turns out that the behavior has yet to be substantiated (Cranbrook and Kemp, 1995. Ibis 137:588–589).

Hornbills are cavity nesters, most taking advantage of natural tree cavities. In the true hornbills, the female seals herself in and undergoes a complete molt of flight feathers during the nesting effort. As a result of their large size and associated need for large trees for their cavity nests and because of the limited distribution of many species, hornbills may be particularly susceptible to becoming endangered as a result of elimination of old growth forest. Range maps are shown for all but the Visayan Wrinkled Hornbill (*Aceros waldeni*), but these are of historic ranges and populations of many species are already fragmented and declining. At least some species will use nest boxes, and an appendix provides guidelines for captive management and breeding. These management tools are, however, just that—tools. They are not answers to long-term survival. Only protection of natural habitats and ecosystems can provide a future for these birds. Kemp acknowledges the use of hornbills as human food and for medicinal and religious purposes in various cultures and suggests that any efforts to manage the species must consider these human needs. Since most of the larger species produce two eggs, but raise only a single chick, he suggests removal of the second chick as one means of meeting these needs.

Tables include a wealth of morphological and ecological data begging for further analysis and comparison with other taxa. Plates include not only superb field guide style composites, showing each species with sex and age variants, but also ones showing all Asian and all African hornbills in flight. Colored photographs illustrate some habitats, nests, and a skull carved by a Chinese craftsman. The bibliography of nearly 600 references includes some unpublished reports and citations from an incredible array of journals and often obscure

series. Certainly, this is a resource that in itself will facilitate further advancement of our knowledge of this group. The three-page glossary defines some hornbill-specific terms and also a strange assortment of other ornithological and non-ornithological (e.g., "selective logging," "swidden agriculture") terms. "Rectrix" is misspelled in the glossary.

"The Hornbills" is obviously a labor of love, dedication, and deep understanding, and I thoroughly enjoyed reading it. It is a model for monographic coverage that would be difficult to surpass.—JEROME A. JACKSON.

WOODPECKERS. By Hans Winkler, David A. Christie, and David Nurney. Houghton Mifflin Company, Boston. 1995: 406 pp., 64 color plates, some black-and-white figures, 214 range maps. $40. (hardcover).—This guide to the woodpeckers of the world follows on the heels of somewhat similarly comprehensive monographs on woodpeckers by Short (1982. "Woodpeckers of the World," Delaware Museum of Natural History Monogr. Ser. No. 4, Greenville, Delaware) and Frugis, Malaguzzi, Vicini and Cristina (1988, "Guida ai Picchi del Mondo. Museo Regionale di Scienze Naturali Monogr VII. Torino, Italy." In Italian.). How does Winkler et al. compare to these other monographs?

Winkler et al. recognize 214 species, following the systematic arrangement of Sibley and Monroe (1990. "Distribution and Taxonomy of Birds of the World." Yale Univ. Press, New Haven), which was based largely on Short (1982). Short and Frugis et al. recognize "about" 200 species, with Frugis et al. following Short closely. The taxonomic differences in Winkler et al. result in general from recognition of Short's subspecies of two piculets and several woodpeckers as distinct species.

Introductory material in Winkler et al. includes 35 pages that describe the layout of species accounts, the nature of taxonomic decisions made, descriptions of tribes and genera of woodpeckers, basic zoogeography, morphology, plumages and molt, foods and foraging, habitats, ecology, behavior, and interactions with man. Short's introductory coverage is similar in scope and depth; Frugis et al. is a skeleton by comparison, covering a similar scope of material in much less depth but including useful drawings illustrating foraging patterns and a bit more discussion of conservation problems than found in introductory material of the others.

Color plates by Nurney in Winkler et al. include several species/subspecies per page in somewhat field guide fashion. These focus primarily on adult males but also show heads of adult females. The plates in general are excellent, although the bills of *Campephilus* species seem too slender and "weak." Detailed captions face each plate; captions in the other books are essentially limited to species identification. The plates by Sandstrom in Short (1982) are larger but with generally fewer species per page, sometimes showing species-specific habitat characteristics. The plates by Cristina and Vicini in Frugis et al. often include only one or two species per page, are generally adequate but less refined, and not as well reproduced as in the other books. The plates in Short and Frugis et al. focus only on adult males.

Species accounts in Winkler et al. include a range map, statement of identifying characteristics and distribution, description of habitat, sex and age differences, geographic variation, sample measurements, and descriptions of voice, habits, food, and timing of breeding. Short's species accounts provide a similar range and depth of information. Species accounts in Frugis et al. include both English and Italian common names, listing of subspecies, and very brief descriptions of distinctive characteristics, habitat, distribution, and for some species, notes on behavior and diet. There are no range maps in either Short or Frugis et al.

In format and in being more recent, Winkler et al. have the most useful and comprehensive of these monographs. Their "Woodpeckers" is much more than indicated by the subtitle on

the dust jacket (one of three subtitles used!): "An Identification Guide to the Woodpeckers of the World." All of these books are useful introductions to the diversity, behavioral ecology, and adaptive strategies of the Picidae. Frugis et al. was intended only as an illustrated checklist of the woodpeckers of the world, and it succeeds quite well in that. In comparing the two more comprehensive books, however, one must also consider the backgrounds of the authors, for these certainly have influenced the nature of the finished products. Winkler has studied woodpeckers in many parts of the world and has emphasized vocalizations in much of his work. As might be expected, text material for European species is much stronger. Short has spent a lifetime studying woodpeckers throughout the world with an emphasis on taxonomic studies. His studies in the New World and in Africa have been extensive and are strongly reflected in his monograph.

Having established the similarities and differences in these works, I will now focus on the details included in Winkler et al. With the incredible amount of information included in Winkler et al., some problems could be expected and some are present. On p. 12, the authors refer to *Dryocopus magellanicus* as the Magellanic Woodpecker, stating that it is "often seen as a good intermediate between *Dryocopus* and *Celeus*. . ." Surely this is in error, since elsewhere throughout the book (and among other authors) the Magellanic Woodpecker is treated as *Campephilus magellanicus*. Furthermore, the species generally considered intermediate to *Dryocopus* and *Celeus* is *Dryocopus galeatus*, the Helmeted Woodpecker, a species with very limited range in Brazil, Paraguay, and Argentina.

As a measure of accuracy, I most carefully examined accounts of species with which I had the greatest familiarity. These accounts were generally very good with very up-to-date information, but I found several minor problems with the Red-cockaded Woodpecker (*Picoides borealis*) account. The range map for this species appropriately shows a very fragmented distribution but inappropriately seems to show the species still occupying Missouri, Tennessee, and Maryland and a much wider range in Kentucky than has ever been known. It also shows the species absent from some areas of the mid-South where it is known. In the caption for Plate 34, in reference to the adult female Red-cockaded Woodpecker, the authors indicate that this is the "only 'ladder-backed' species in its range." Since this is a guide intended for identification, and since this species is considered endangered, it is important to note the "ladder back" of the very common Red-bellied Woodpecker (*Melanerpes carolinus*) which occurs throughout the range of the Red-cockaded. Finally, the list of pine species used as nest sites by the Red-cockaded is incomplete (e.g., *Pinus virginiana* isn't included) and seems to inappropriately downplay the importance of loblolly pine (*Pinus taeda*) relative to others.

Another problem is the perpetuation of the notion that juvenile female Hairy Woodpeckers (*Picoides villosus*) normally have an "orange-red patch on crown" (pp. 35, 291). The females very rarely have even a reduced orange-red patch. Eye color mentioned for the Ivory-billed Woodpecker (*Campephilus principalis*) follows Short (1982) and is given as "white to creamy-white" (p. 354), whereas numerous specimen labels and descriptions of early naturalists who closely observed the species almost always refer to the yellow color of the iris. The range map for the Pileated Woodpecker (*Dryocopus pileatus*) shows the species much farther north than it is known to occur in Canada. These are all minor problems that are sometimes ambiguous or incorrect elsewhere in the literature, illustrating that there is still much to be learned about woodpeckers.

In general, "Woodpeckers" is an up-to-date and thorough compendium of information about the world's woodpeckers. It is put together in a user friendly format with good documentation and outstanding illustrations. Winkler et al. have brought us to a new plateau in our understanding of woodpeckers and have made it easier for us to surge on ahead.—Jerome A. Jackson.

ENDANGERED ECOSYSTEMS OF THE UNITED STATES: A PRELIMINARY ASSESSMENT OF LOSS AND DEGRADATION. By Reed F. Noss, Edward T. LaRoe III, and J. Michael Scott. U.S. Department of the Interior, National Biological Service, Biological Report 28, Washington, D.C.1995: 58 pp., three numbered text figs., eight black-and-white photographs with captions, five appendices, no charge (paper).—The status of natural ecosystems throughout the United States is currently a topic of considerable concern. Unfortunately, minimal information is available to determine the geographical extent and condition of the ecosystems of the United States, and the quality of information varies greatly from state to state. In spite of these difficulties, Noss et al. have done a superb job of defining ecosystems to evaluate and compiling and analyzing large databases in order to estimate the loss and degradation of United States ecosystems. The authors' arguments for managing and protecting ecosystems to prevent the necessity to have to deal with threatened and endangered species focuses on the primary problem of endangered species management.

The booklet is well written and treatments of topics are presented clearly in a logical fashion. The authors list ecosystems as critically endangered (30), endangered (58), or threatened (38), with the real "meat" of the publication located in the appendices where the extent of loss for each ecosystem is presented. The authors indicate that degradation and losses of ecosystems have been most pronounced in the South, Northeast, Midwest, and California. Also evaluated is the potential risk for further loss within each ecosystem. Because pristine sites of many ecosystems are already nearly nonexistent, the authors suggest that restoration be an integral part of ecosystem management. The authors show where significant information gaps occur. The illumination of these gaps should help state and federal agencies adjust methodologies and priorities for data collection. This publication is essential for researchers and managers who work with threatened, endangered, or sensitive species and any aspect of ecosystem management. The authors should be commended for this excellent publication.—RICHARD N. CONNER.

THIS FRAGILE LAND. A NATURAL HISTORY OF THE NEBRASKA SANDHILLS. By Paul A. Johnsgard. Univ. Nebraska Press, Lincoln, Nebraska. 1995:xv + 256 pp. 48 numbered figs., 5 tables. $35.00 (cloth).—Warning! Read this book and you will never again travel across the Great Plains on I80 single-mindedly driven by purple mountains majesty over the western horizon. You will be obliged to make a significant diversionary journey northward into the largest area of sand dunes in the Western Hemisphere. But once on the blue highways, of which there are very few, you will discover, as Johnsgard writes, "Most roads in the sandhills lead nowhere." But that is their charm, "a land of no straight lines . . . patiently shaped by water, wind, and time." It's a landscape laid down in the Miocene, formed during the post-glacial, stabilized by prairies, richly endowed with rivers, brooks, fens, and marshes and with a human population of about one person per square mile. This is an ecological natural history that illustrates the diverse biotic communities in a region that comprises almost a quarter of the area of the state. While grasshoppers and grasshopper mice (complete with sonogram), midges, and sticklebacks (yes, they do it in Nebraska just like they do it for European ethologists) are described, birds are well represented, including some bird transect data gathered by H. Elliot McClure in the mid-1940's. Part One takes you around the periphery—the valley of the Niobrara, the (ponderosa) pine ridge and High Plains, the Platte, tallgrass prairie, and cornfields. Part Two takes you into the interior with chapter subtitles such as "Sandreed, Sicklebills, and 'Roo Rats;" "Boots, Burrowing Owls and Box Turtles;" "Whispers, Bells, and Trumpets." Part Three describes the advent of the ranching economy in the nineteenth century and the development of center-pivot irrigation during

the last third of the twentieth century. Irrigation has not depressed the water table very much because of the rapid recharge rates; but as a consequence of the ease at which water returns to the aquifers deep in the sand, irrigation has led to widespread ground-water pollution by nitrates, herbicides, and pesticides. But there is hope. Johnsgard tells us that the people who are making their living in the sandhills have banded together to thwart external economic and political pressures to increase short-term profit at the expense of long-term productivity. The seven appendices in the book comprise 30% of its length and provide, for example, a checklist of the vertebrates and vascular plants indicating the biotic communities in which they occur, a distributional list of sandhills birds, an annotated list of natural areas in the sandhills, and a very helpful glossary. Most of you have read other books by the author. This is Johnsgard at his poetic best, not only in the prose, but also in his delightful line drawings that complement the text.—JOHN L. ZIMMERMAN.

WHERE TO WATCH BIRDS IN SOUTH AMERICA. By Nigel Wheatley. Princeton Univ. Press, 41 William St., Princeton, New Jersey 08540. 1995: 431 pp., 52 black-and-white bird figs., 108 maps, $35.00 US (hardback).—This is a highly useful work that discusses an entire continent and related offshore archipelagos. As some recent books on South American birds have ignored the Galapagos and Falklands, it was good to see them included. Each country (and archipelago) has an introduction, with notes on size, getting around, lodging and food, health and safety concerns, climate and best months to visit, habitats, and conservation; along with country species totals, highlights, and endemic species. The author is a numbers gatherer with many accountings and tables of birds and endemic families per country; species numbers per size of country; statistics on trip lists, day lists; top ten sites for species lists; and endemic family lists per country. The most useful lists are each country's endemics with brief notes on where such endemics are found (with 179 in Brazil, for instance).

The sites within each country are clustered, rather than alphabetized, and well-labeled and numbered in each country's locator map. The nearly 100 site maps are well executed. One would wish that there were maps for all 206 sites. A typical site account has a good introduction, separate lists of endemics, specialties, others (birds), other wildlife (usually a few mammals, good feature), and access notes. Many sites are published for the first time in a book with broad availability.

The highly competitive business of bird listing companies competing with each other for the same clients has led to many great spots being kept semi-secret. Independent travelers have often remarked on how rarely they weaseled information out of such companies or their trip leaders. Some tips on where to go would end up on competitor's itineraries. The outdated code of ethics that birders must share all finding information with no charge for cost of gathering or preparing such information for strangers was in place before the tour businesses. Grossly underpaid bird tour leaders pay top dollar for legal, medical, financial and other consulting advice, but when those same professionals are birders they demand our consulting advice for free. This book will save tour leaders countless hours of *pro bono* work answering the questions so well answered in this work.

The actual species lists given for each locale are confusingly broken up into three categories. What a pain to have to search through three incomplete lists running like prose text. I would have much preferred two columns side-by-side with annotations as to endemics, specialties, and others (via bolds and italics), along with crude abundance symbols (where such information is available). As "no one reads introductions," the reader will have a hard time figuring out what the asterisks mean (tip: it's buried on page 18). Space does preclude complete lists in a book treating an entire continent, but I felt that North American migrants and winterers were rarely covered.

How good are the locale lists? To answer this, I compared my notes from three recent annual visits to the excellent Costanera Sur Faunal Reserve adjacent to downtown (city centre) Buenos Aires, Argentina. Taking civilized non-birders en route to Antarctica at mid-morning and mid-afternoon hours, with no tapes or playbacks, and without wading in the marshes, I found 82 species. We saw four of his 12 specialties listed, 36 of his 51 "Others," and 42 species not mentioned. The author does state that common and widespread species are purposely left off such lists. Not listed in the book were such species as White-faced Ibis (*Plegadis chihi*) (much commoner than two other ibises listed), the "southern" endemic Coscoroba Swan (*Coscoroba coscoroba*) (large numbers in "dry" years), Red Shoveler (*Anas clypeata*) (always there), rarities such as Masked Duck (*Oxyura dominica*) and Pampas Paintedsnipe (*Nycticryphes semicollaris*) and interesting common species for first-time visitors such as Rufous Hornero (*Furnarius rufus*) and Chalk-browed Mockingbird (*Mimus saturninus*).

Ornithologists should note that not a single scientific name appears in the book; other checklists will have to be handy. Fortunately, South America was nearly devoid of British colonies and a confusing plethora of "common" names in English (as has existed in Africa and Asia) did not evolve. Common sense common names with unique modifiers that tied species to "correct" group-names were agreed upon in an early (recent) period by several American ornithologists. It is interesting to note that it was a British birder who put together this work despite the much greater number of Americans traveling there. As expected, there was no mention of the *Malvinas* name in the Falklands chapter. There was also no mention of the 22 pioneering chapters on South America in "Finding Birds Around the World" (Peter Alden and John Gooders, Houghton Mifflin, Boston, 1981).

Mistakes of commission appeared few. Like so many writers, he says the train climbs UP to the ruins of Machu Picchu (7374 feet) from Cusco (10,200 feet) in Peru. Listing of significant inbound tour operators and lodge addresses is most useful, although I doubt the Venezuelan Audubon Society is the main avenue for booking Hato Pinero in the llanos. The listing of Antarctic ships in this 1995 guide has no mention of the new inexpensive Russian ships on the scene for several years, while mentioning the Ocean Princess which has been out of service since April 1993.

Despite the high price tag for a book with no color plates, this is a work that will repay its cost easily in directing casual and serious visitors to the most representative accessible parks and wild areas on the bird continent.—Peter Alden.

A guide to the birds of Mexico and northern Central America. By Steve N.G. Howell and Sophie Webb. Oxford Univ. Press, New York. 1995. 1,010 pp., 1087 maps, 71 color plates, 44 linecuts. $39.95 paper, $75.00 cloth.—This long awaited handbook covers all birds known from Mexico, Belize, Guatemala, Honduras, and western Nicaragua. The fine color plates by Sophie Webb cover many plumages and subspecies for the first time. The plates in my copy appear to be overexposed, as the colors seem a bit washed out compared to some originals I've seen. Most North American winterers are not illustrated, so that visitors will again have to take along one of the North American field guides. The range maps (all at the species level) are excellent and show where birds are present in migration, as well as breeding and wintering areas. These maps are done on an outline of provinces which is far better than doing so with a few rivers or no provinces as some books present them. The species accounts are exhaustive, with good attention to vocalizations, similar species, ranges, relative abundances, habitats, taxonomic questions, and major subspecies. With such excellent plates, it appears that the descriptions are too long. Every shade,

streak, and pattern is included in minute detail, often running on for many hundreds of words.

Steve N. G. Howell, from Britain, embarked on this project in November 1981 and proceeded to spend the better part of the next dozen years gathering identification, ecological, distribution, and vocalization information in thousands of sites in the field. Based at the Point Reyes Bird Observatory, he queried hundreds of (chiefly American) colleagues for details (note the five pages of acknowledgments) and supervised the production of plates and range maps. Most of the field guide work in Latin America has focused on areas from Costa Rica southward since the early 1970s when no less than four were published on the Mexico/Guatemala region. It is so nice to see such a compendium of knowledge come out on this area after a gap of roughly 20 years, especially since this area is an important one for wintering Nearctic birds, contains many endemics and has a rapidly diminishing stock of pristine habitat.

The book suffers from an overuse of abbreviations, and the various keys to this plethora of them are scattered in too many places. Some abbreviations are listed on unnumbered page 87, some on unnumbered pages xv and xvi, others in acknowledgments (by extrapolation), and others such as INIREB, ICACH, RSMHN, and SEDUE, on page 798. They should all have been listed from A–Z on both endpapers for reference. Why can't Chiapas be Chia instead of Chis? Couldn't FCUNAM be shortened somehow? Under each species account the sections are split up into ID, SS, SD, RA, and NB, which could have been spelled out or at least given as Ident., Sim. sp., Status, Distr., Range and Note. In a short sample species account such as Worm-eating Warbler *Helmitheros vermivorus* the reader will have to translate ID, SE, SD, F, C, S, Ver, U, R, S, Tamps, Nay, PA, SNGH, PP, F, U, NE, R, W, DF, RA, E, and SE. This makes for unpleasant reading. It took a long time to figure out what the asterisk indicated. On page 87 you will find that it means different things depending on where it is placed.

The maps on pages 2–6 appear to have enough space to have most names of islands, provinces, and selected cities and towns written out at the correct site rather than resorting to a endless letters and numbers. The biogeographic maps on pages 8–9 are yet another nightmare of letters and numbers. Despite this, the geography and bird distribution section is well organized. The various tables on migration, visitors and species that withdraw from parts of ranges are of great interest. Note that all the microscopic asterisks are actually tiny letter a, b, and c symbols explained on page 35. I was pleased to see the country-by-country chapters on conservation. Maps showing sites of present day reserves would have been helpful.

Rare indeed these days is the author of regional guides who fails to "lump and split" any number of species and attempt to improve English names. This book is no exception. The sequence of orders and families follows the A.O.U. Checklist of North American Birds (1983) rather than the more controversial DNA-DNA sequence. The "lumping/splitting" pendulum swings over to splits here with four species created out of the Green Parakeet (*Aratinga holochroa*) and four species created out of the Fork-tailed Emerald (*Chlorostilbon canivetii*). There are several dozen other accepted splits involving such genera as *Amazona* parrots, *Glaucidium* pygmy-owls, *Caprimulgus* nightjars, *Campylopterus* sabrewings, *Cynanthus* and *Amazilia* hummingbirds, *Trogon, Formicarius* ant-thrushes, *Platyrinchus* spadebills, *Progne* martins, *Stelgidopteryx* swallows, *Hylorchilus* and *Troglodytes* wrens, *Vireo, Icterus* orioles, and *Junco*. The Yellow-rumped Warbler (*Dendroica coronata*) is not divided. Many birders will be surprised to see the flowerpiercer genus *Diglossa* placed in the *Emberizinae*.

As for English names he fails to use Louisiana Heron as a good alternate to Tricolored Heron (*Egretta tricolor*), coins Eared Quetzal (better than Trogon) for *Euptilos neoxenus*,

and fails to adopt Whitestart for *Myioborus*. Members of *Myioborus* genus (all of which have white outer tail feathers) have no red in the tail and should not retain the grossly incorrect name applied to Old World thrushes of the genus *Phoenicurus*. I note that the silver-like color is spelled grey. An informal group of ornithologists involved with English names in the 1980's proposed that the Americans might use grey (not gray) in return for the British dropping the use of the u in colour and harbour.

Useful appendices include lists of species known from islands and cays of both the Pacific and Atlantic coasts, descriptions of fifty species of eastern Honduras that are omitted from the main text, and a 26 page bibliography that somehow omits my "Finding Birds in Western Mexico" (University of Arizona Press, Tucson, 1969) that would have been listed first!—PETER ALDEN.

CURRENT ORNITHOLOGY. Volume 12. Dennis M. Power (ed.). Plenum Press, New York, New York. 1995:278 pp.$79.50.—Plenum Press continues to provide outstanding service to the community of scientific ornithologists by publishing this series. The present volume includes chapters on (1) testosterone and polygyny in birds by Les D. Beletsky, David F. Gori, Scott Freeman, and John C. Wingfield, (2) use of migration counts to monitor landbird populations by Erica H. Dunn and David J. T. Hussell, (3) ptilochronology by Thomas C. Grubb, Jr., (4) individual voice discrimination by Marcel M. Lambrechts and Andre A. Dhondt, (5) evolution of bird coloration and plumage elaboration by Udo M. Savalli, and (6) hatching asynchrony and the onset of incubation by Scott J. Stolcson and Steven R. Beissinger. As has been true in all previous volumes, the editing and writing of these chapters is excellent and the content remarkably good, particularly given the length of the series.

I will not describe the contents of the chapters here as the titles pretty much tell the story. The accounts on migration and hatching asynchrony were particularly interesting to me and promise to have wide application in ornithology. The chapters on voice discrimination, evolution of color, and ptilochronology forced me to revise and expand my course notes for my university class in ornithology. The chapter on polygyny illustrates how physiology and behavior can be integrated to better understand birds. As usual, these sources are a gold mine for researchers, graduate students, and teachers.—C. R. BLEM.

LAST OF THE CURLEWS. By Fred Bodsworth. Counterpoint, Washington D.C. 1995. $15 (cloth).—This little book of less than a hundred pages has become a conservation classic since it was published in 1955 by Dodd, Mead & Company. This edition has been expanded by including a Forward by Pulitzer Prize-winning poet and conservationist W.S. Mervin, a brief Epilogue by Bodsworth, and a 45 page Afterword by Nobel Prize-winning particle physicist Murray Gell-Mann. Gell-Mann's Afterward begins with the question: "Can the human race learn, while there is still time, how to coexist with the great diversity of bird life on this planet?" In the pages which follow, he examines the question of extinction in the context of geologic time and past periods of catastrophic extinction of species and then focuses on the changes to the biosphere which humans have produced in the past few centuries and the enormous stress we continue to put on the ecological systems of the planet. He eventually enters an arena which is perhaps best described as philosophical or political with a discussion of quality of human life versus quantity, at one point asking: "Why squander quality of life for the sake of mere numbers of humans?" In a world already overcrowded with humans, this is perhaps the most fundamental question one could ask.

The book itself contains 11 chapters which comprise a biographical sketch of the hypothetical "last of the curlews," an Eskimo Curlew (*Numenius borealis*). It is a touching story told by a biologist with a deep understanding of shorebird biology. The skillful avoidance of anthropomorphism is quite remarkable, as is the author's use of language to evoke an emotional response from the reader. The chapters are separated by short sections entitled "The Gantlet" [gauntlet] which consist of vignettes quoted from published historical documents which delineate the slaughter of Eskimo Curlews by man and the virtual disappearance of the species.

This classic story of human exploitation and extinction, together with the penetrating analysis of global problems by Gell-Mann, are well worth reading and discussing, particularly in times of political and economic change.—WILLIAM E. DAVIS, JR.

Erratum

In the paper "Detectability and population density of Scaly-naped Pigeons before and after Hurricane Hugo in Puerto Rico and Vieques Island," (Wilson Bulletin, 107[4]:727–733), the first sentence should be: "Hurricane Hugo hit northeastern Puerto Rico with sustained winds of 30–40 m/s (gusting to 50–60 m/s) on 18 September 1989 (see Boose et al., 1994)."

INFORMATION FOR AUTHORS

The Wilson Bulletin publishes significant research and review articles in the field of ornithology. Mss are accepted for review with the understanding that the same or similar work has not been and will not be published nor is presently submitted elsewhere, that all persons listed as authors have given their approval for submission of the ms, and that any person cited as a personal communication has approved such citation. All mss should be submitted directly to the Editor.

Text.—Manuscripts should be prepared carefully in the format of this issue of *The Wilson Bulletin*. **Mss will be returned without review if they are not properly prepared.** They should be neatly typed, double-spaced throughout (including tables, figure legends, and "Literature cited"), with at least 3 cm margins all around, and on one side of good quality 8.5″ × 11″ paper. Do not use erasable bond. **Mss typed on low-quality dot-matrix printers are not acceptable.** The ms should include a cover sheet (unnumbered) with the following: (1) Title, (2) Authors, their institutions, and addresses, (3) Name, address, and phone number of author to receive proof, (4) A brief title for use as a running head. All pages of the text through the "Literature cited" should be numbered, and the name of the author should appear in the upper right-hand corner of each. The text should begin in the middle of the first numbered page. Three copies should be submitted. Xerographic copies are acceptable if they are clearly readable and on good quality paper.

Tables.—Tables are expensive to print and should be prepared only if they are necessary. Do not repeat material in the text in tables. Tables should be narrow and deep rather than wide and shallow. Double space all entries in tables, including titles. Do not use vertical rules. Use tables in a recent issue of the *Bulletin* as examples of style and format. Tables should be typed on separate unnumbered pages and placed at the end of the ms.

Figures.—**Illustrations must be readable (particularly lettering) when reduced in size.** Final size will usually be 11.4 cm wide. Illustrations larger than 22 × 28 cm will not be accepted, and should be reduced photographically before submission. Legends for all figures should be typed on a separate page. Photographs should be clear, of good contrast, and on glossy paper. Drawings should be in India ink on good drawing board, drafting paper, or blue-lined graph paper. Figures produced by high-quality laser printers may be acceptable. All lettering should be done with a lettering instrument or printer. Do not use typewriter lettering and do not submit figures having adhesive transfer letters affixed to them. Designate the top of each illustration and label (on the back in soft pencil) with author's name, ms title, and figure number. Submit two duplicates or readable xerographic copies of each figure as well as the original or high-contrast glossy photo of the original.

Authors of accepted papers are urged to submit voucher photographs of their work to Visual Resources for Ornithology (VIREO) at the Academy of Natural Sciences of Philadelphia. Accession numbers from VIREO will then be published within appropriate sections of the paper to facilitate access to the photographs in subsequent years.

Style and format.—The current issue of *The Wilson Bulletin* should be used as a guide for preparing your ms; all mss must be submitted in that format. For general matters of style authors should consult the "CBE Style Manual," 5th ed., Council of Biology Editors, Inc., Bethesda, MD, 1983. Do not use footnotes or more than two levels of subject subheadings. Except in rare circumstances, major papers should be preceded by an abstract, not to exceed 5% of the length of the ms. Abstracts should be informative rather than indicative, and should be capable of standing by themselves. Most units should be metric, and compound units should be in one-line form (i.e., $cm\text{-}sec^{-2}$). The continental system of dating (19 Jan. 1950) and the 24 hour clock (09:00, 22:00) should be used, and the Standard Time specified (e.g., EST for Eastern Standard Time) at first reference.

References.—In both major papers and general notes, if more than four references are cited, they should be included in a terminal "Literature cited" section. Include only refer-

ences cited in the ms, and only material available in the open literature. ("In-house" reports and the like should not be cited.) Use recent issues of the *Bulletin* for style, and the most recent issue of "BIOSIS," BioScience Information Service, Philadelphia, PA, for abbreviations of periodical names. If in doubt, do not abbreviate serial names. Manuscripts with fewer than five references should be cited internally, e.g., (Sprenkle and Blem, Wilson Bull. 96:184–195) or Sprenkle and Blem (Wilson Bull. 96:184–195).

Nomenclature.—Common names and technical names of birds should be those given in the 1983 A.O.U. Check-list (and supplements as may appear) unless justification is given. For other species the *Bulletin* uses the common names in Sibley and Monroe, "Distribution and Taxonomy of Birds of the World." Common names of birds should be capitalized. The scientific name should be given at first mention of a species both in the abstract and in the text.

The editor welcomes queries concerning style and format during your preparation of mss for submission to the *Bulletin.*—Charles R. Blem, Editor.

This issue of *The Wilson Bulletin* was published on 1 June 1996.

The Wilson Bulletin

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The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 108, NO. 3 SEPTEMBER 1996 PAGES 397–606

(ISSN 0043-5643)

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THE WILSON BULLETIN
(ISSN 0043-5643)

THE WILSON BULLETIN (ISSN 0043-5643) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th Street, Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Periodicals postage paid at Lawrence, KS. POSTMASTER: Send address changes to THE WILSON BULLETIN, P.O. Box 1897, Lawrence, KS 66044-8897.

Back issues or single copies are available for $12.00 each. Most back issues of the *Bulletin* are available and may be ordered from the Treasurer. Special prices will be quoted for quantity orders.

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Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

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Frontispiece. Adult (right) and juvenile (left) *Acrobatornis fonsecai,* Pink-legged Graveteiro, a new genus and species in the Furnariidae from southeastern Bahia, Brazil. Painting by Paul Donahue.

THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Society

VOL. 108, NO. 3 SEPTEMBER 1996 PAGES 397–606

Wilson Bull., 108(3), 1996, pp. 397–433

A NEW GENUS AND SPECIES OF FURNARIID (AVES: FURNARIIDAE) FROM THE COCOA-GROWING REGION OF SOUTHEASTERN BAHIA, BRAZIL

JOSÉ FERNANDO PACHECO,[1] BRET M. WHITNEY,[1,2] AND LUIZ P. GONZAGA[1]

ABSTRACT.—We here describe *Acrobatornis fonsecai*, a new genus and species in the Furnariidae, from the Atlantic Forest of southeastern Bahia, Brazil. Among the outstanding features of this small, arboreal form are: black-and-gray definitive plumage lacking any rufous; juvenal plumage markedly different from adult; stout, bright-pink legs and feet; and its acrobatic foraging behavior involving almost constant inverted hangs on foliage and scansorial creeping along the undersides of canopy limbs. Analysis of morphology, vocalizations, and behavior suggest to us a phylogenetic position close to *Asthenes* and *Cranioleuca*; in some respects, it appears close to the equally obscure *Xenerpestes* and *Metopothrix*. New data on the morphology, vocalizations, and behavior of several furnariids possibly related to *Acrobatornis* are presented in the context of intrafamilial relationships. We theorize that *Acrobatornis* could have colonized its current range during an ancient period of continental semiaridity that promoted the expansion of stick-nesting prototypes from a southern, Chaco-Patagonian/Pantanal center, and today represents a relict that survived by adapting to build its stick-nest in the relatively dry, open, canopy of leguminaceous trees of the contemporary humid forest in southeastern Bahia. Another theory of origin places emphasis on the fact that the closest relatives of practically all (if not all) other birds syntopic with *Acrobatornis* are of primarily Amazonian distribution. *Acrobatornis fonsecai* has a most unusual distribution in a restricted region in which lowland Atlantic Forest has been converted virtually entirely to cocoa plantations. Until very recently a lucrative and vitally important source of income for Bahia, the economic base for cocoa production has suffered catastrophic, apparently irrecoverable, decline owing to "witch's broom" disease, which has proven resistant to all forms of control. The predictable wave to cut and sell the tall trees shading failing cocoa plantations has already begun in earnest with the consequence that the remnant forest canopies in this region, upon which *Acrobatornis fonsecai* is totally dependent, are being rapidly destroyed. This remarkable new furnariid and the secrets it holds for elucidation of phylogeny, evolutionary history, speciation patterns, and zoogeography, if not safeguarded immediately, when its habitat is still for sale, could disappear in the coming decade. *Received 23 April 1996, accepted 21 May 1996.*

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RESUMO.—*Acrobatornis fonsecai,* um novo gênero e nova espécie de Furnariidae, é descrito da Mata Atlântica do sudeste da Bahia, Brasil. Dentre os aspectos notáveis desta pequena ave arborícola estão: a sua plumagem definitiva cinza e preta sem qualquer avermelhado; plumagem juvenil bem diferenciada da adulta; patas e pés fortes de coloração rosa vivo; e seu comportamento acrobático de forrageamento de envolve uma quase permanente posição invertida dependurada na folhagem e uma "escalada negativa" ao longo das superfícies inferiores dos galhos da copa. Através de análises da morfologia, vocalizações, e comportamento, é sugerido uma posição filogenética de *Acrobatornis* próximo aos *Asthenes* e *Cranioleuca*; em alguns aspectos o novo gênero mostra-se próximo aos igualmente obscuros *Xenerpestes* e *Metopothrix.* Novos dados sobre a morfologia, vocalizações, e comportamento de vários Furnariidae relacionados a *Acrobatornis* são apresentados no contexto das afinidades intrafamiliares. É teorizado que *Acrobatornis* colonizou sua atual área de distribuição durante um período remoto de semi-aridez continental, que promoveu a expansão oriunda do sul, Chaco e Patagônia, dos protótipos construtores de ninhos de graveto. Ele hoje representaria uma "relíquia" que conseguiu sobreviver, no sudeste da Bahia, ao período úmido contemporâneo, por adaptar construir seu ninho de gravetos nas copas relativamente secas e abertas das árvores leguminosas. Uma outra teoria sobre a origem enfatiza o fato de que os parentes mais próximos de quase a totalidade (se não todos) das aves sintópicas com *Acrobatornis* possuem uma distribuição principalmente amazônica. Num padrão incomum de distribuição, *Acrobatornis fonsecai* ocorre numa região restrita da Mata Atlântica de tabuleiro do sudeste da Bahia, que tem sido quase completamente convertida em plantações de cacau. A cacauicultura, até muito recentemente lucrativa e substancial fonte de receita para a Bahia, tem sofrido um catastrófico, aparentemente irrecuperável, declínio na produção devido à disseminação da "vassoura-de-bruxa," doença causada por fungos, que tem resistido a diversas formas de controle. De maneira grave, as grandes árvores copadas, remanescentes da floresta íntegra, das quais *Acrobatornis fonsecai* é totalmente dependente, já estão sendo cortadas e vendidas. Este notável novo furnarídeo, e os segredos que ele guarda para elucidação da filogenia, história evolutiva, padrões de especiação e zoogeografia, se não imediatamente salvaguardados, quando o seu hábitat ainda está à venda, poderão desaparecer na próxima década.

From a continental perspective, the Neotropical family Furnariidae has undergone a geographical and ecological radiation, paralleled by a diversity of form and function, without equal in the world of birds. The Furnariidae contains more than 230 species in 53 genera (as currently defined; Sibley and Monroe 1990, 1993). To this magnificent assemblage we must now add one more genus and species, a member of such singular appearance, ecology, and distribution as to mark it truly outstanding even in a family characterized by adaptive extremes. Perhaps most remarkable, however, is our discovery of this new form in the remnant Atlantic Forest of southeastern Bahia, a heavily populated region in which we never would have predicted the contemporary existence of a furnariid of such affinities.

On 26 January 1988, in search of habitat that might harbor the little-known Stresemann's Bristlefront (*Merulaxis stresemanni*), Whitney located a slope cloaked in undisturbed Atlantic Forest in the serra das Lon-

tras above the village of Itatingui in the cocoa-growing region of southern Bahia. Although observations were precluded by rain, the area was targeted for a detailed avifaunal survey. In November 1994, following an ornithological investigation of selected points in interior Minas Gerais and Bahia ending in the city of Salvador, Whitney suggested to Pacheco and Paulo Sérgio M. da Fonseca that they make an introductory visit to Itatingui along their return drive to Rio de Janeiro. Documentation of a largely unknown avifauna in Atlantic Forest fragments in the highest parts of the serra de Ouricana approximately 125 km WNW of Itatingui (Gonzaga et al. 1995), and recent discoveries of undescribed species there (Gonzaga and Pacheco 1995, Pacheco and Gonzaga 1995), indicated an urgent need to explore the Atlantic Forest of southern Bahia north of the Rio Jequitinhonha and interior from the relatively well known coastal forests. Thus, on the morning of 17 November 1994, while observing birds in a mixed-species flock foraging in the canopy of trees shading a cocoa plantation at the edge of undisturbed forest above Itatingui, Fonseca called Pacheco's attention to a strange pair of birds, one gray-and-black and the other largely brown, creeping along the undersides of limbs, and hanging acrobatically on clusters of foliage and flowers of a tall *Croton* tree. They were able to observe the birds for several minutes, noting details of the plumage and foraging behavior. It was clearly a species unknown from Brazil, and quite possibly unknown altogether. After discussion of this exciting news with Gonzaga and Whitney, Pacheco, Fonseca, and Claudia Bauer returned to Itatingui in late January 1995 and obtained four specimens, including two of each "morph" they had identified previously.

It was clear even on cursory inspection that the specimens represented a species unknown to science, and further examination indicated a strong probability that a new genus would have to be erected as well. Rather than describe the new form immediately, it was decided to return to Itatingui in October, when the birds would likely be breeding and vocal, so that more ecological and distributional information could be gathered. Thus, from 2 to 12 October 1995, Pacheco, Fonseca, Whitney, and Barth explored the serra das Lontras above Itatingui, and a number of other localities in the general region. This expedition was highly successful, resulting in: the discovery and collection of the nest and the location of 52 additional nest sites which defined, we think to a large extent, the distributional limits of the new bird; the tape-recording of several individuals, which documented the vocal repertoire of the species almost completely; the tape-recording and collection of two additional voucher specimens, which permitted preparation of a skeleton and preservation of additional biochemical material; and the production of photographs and

FIG. 1. Adult *Acrobatornis fonsecai,* gen. nov. sp. nov. Video image captured from Hi-8 format original (11 Oct. 1995 near Camacan, Bahia; video by Whitney).

video recordings of habitat, nests, and foraging maneuvers. Furthermore, we determined that the known distribution of the new species was entirely coincident with the cocoa-growing province of southern Bahia—the consequences of which appear to be devastating for the continued survival of the new bird. Finally, in March 1996, Whitney located the new species at additional localities in the cocoa-growing region slightly north and west of previously documented ones.

Consideration of all these data, informed through extensive personal field experience with the Furnariidae, including all but one genus and 11 currently recognized species, and comparison with museum anatomical and skin specimens from a cross-section of potentially related genera, convinces us that the unknown form indeed represents a new genus and species in the Furnariidae. The descriptions follow.

Acrobatornis gen. nov.

TYPE-SPECIES: *Acrobatornis fonsecai* Pacheco, Whitney, and Gonzaga.

DIAGNOSIS.—A small, arboreal furnariid (weight 14 g) completely lacking rufous in definitive plumage, and largely orange-tawny in juvenal plumage. Adults basically gray with black wings, tail, and cap (Frontispiece, Fig. 1). Tail shorter than the wing (with tail/wing ratio varying from 0.86 to 0.92, with an average of 0.89); strongly graduated and slightly

stiffened, composed of 12 rectrices. Two inner pairs of rectrices strongly acuminate at the tips and deeply excised on the inner web; the acumination at the tips of the rectrices decreases gradually from innermost to outermost, so that outermost are almost blunt, cuneiform in shape and only slightly excised on the inner web. Outer pair of rectrices about 60% of the length of the innermost pair, and projecting far beyond the under tail coverts. Wing relatively long in comparison to most furnariids of similar mass, and extending well beyond base of the tail. Seventh to ninth primaries longest and approximately equal in length; sixth primary only slightly shorter; tenth and fifth primaries of nearly equal length and about 5 mm shorter than longest ones.

Bill compressed, short and pointed; culmen slightly decurved, skull pseudo-schizorhinal (Fig. 2A). Tarsi short and strong (Fig. 2A), conspicuously pink-colored. Hind toe thicker than front toes; claw of hind toe slightly shorter than the length of the toe itself. Sternum two-notched. Syrinx typically furnarioid, with well-defined Membranae tracheales, Processi vocales without "horns," and two pairs of intrinsic syringeal muscles (Fig. 3). Membranae tracheales limited posteriorly by A-2 (A-3 vestigial), and anteriorly by a drum formed by the partial fusion of two elements.

SPECIMENS EXAMINED: SKINS.—Only specimens actually measured are listed; many others were compared superficially. *Acrobatornis fonsecai,* gen. nov, sp. nov.: Brazil: Bahia, 2 males (Museu de Zoologia da Univ. de São Paulo [hereafter MZUSP] No. 74154 [holotype], Museu Paraense Emilio Goeldi [hereafter MPEG] No. 52345), 1 female (MZUSP 74155), and 3 sex unk. (MZUSP 74156 [juv.], MPEG 52346 [juv.], and Louisiana State Univ. Museum of Natural Science [hereafter LSUMZ] 160000 [ad.]). *Cranioleuca pyrrhophia*: Bolivia: Santa Cruz, 3 males (LSUMZ 124033, 124036, 124040). *C. curtata*: Peru: San Martín, 1 male (LSUMZ 86368); Pasco, 1 male (LSUMZ 130232); Ayacucho, 1 male (LSUMZ 69428); Bolivia: Cochabamba, 1 male (LSUMZ 37666). *C. pallida*: Brazil: São Paulo, 1 male (LSUMZ 63352). *C. albiceps*: Bolivia: La Paz, 3 males (LSUMZ 95950, 101981, 101983). *Asthenes dorbignyi*: Peru: Arequipa, 2 males (*arequipae*: LSUMZ 114142, 119197); Bolivia: La Paz, 2 males (*consobrina*: LSUMZ 101995, 101996). *A. baeri*: Bolivia: Santa Cruz, 3 males (LSUMZ 153692, 153693, 153698); Argentina: Corrientes, 1 male (LSUMZ 54632); Uruguay: 1 male (Academy of Natural Sciences [hereafter ANSP] No. 169843). *A. patagonica*: Argentina: Chubut, 2 (LSUMZ 73269, ANSP 186350). *Thripophaga fusciceps*: Bolivia: Beni, 2 males, 1 female (LSUMZ 124062, 124063, 124065). *Phacellodomus sibilatrix*: Bolivia: Santa Cruz, 2 males, 1 female (LSUMZ 153700, 153701, 153702); Argentina, Chaco, 1 male (LSUMZ 83932). *P. rufifrons*: Brazil: Minas Gerais, 2 males (LSUMZ 65165, 65166), Mato Grosso, 1 male (LSUMZ 80295); Bolivia: Santa Cruz, 2 males (LSUMZ 124070, 124074). *Siptornis striaticollis*: Peru: Cajamarca, 3 males (LSUMZ 87015, 87016, 87017); Colombia: Huila, 1 male (ANSP 155470). *Xenerpestes minlosi*: Panama: Darién, 1 sex unk., (ANSP 150153); Colombia: Bolivar, 1 female (ANSP 160747). *X. singularis*: Ecuador: Morona-Santiago, 1 female (ANSP 176812), Zamora Chinchipe, 1 female (ANSP 185397); Peru: San Martin, 2 females, 1 sex unk. (LSUMZ 84690, 84691, 84692). *Metopothrix aurantiacus*: Ecuador: Napo, 2 males (LSUMZ 70898, 82963); Peru: Loreto, 1 male (LSUMZ 119657). *Margarornis squamiger*: Bolivia: La Paz, 3 males (LSUMZ 95985, 95989, 95991).

SPECIMENS EXAMINED: ANATOMICALS.—Skulls illustrated: *Acrobatornis fonsecai,* gen. nov., sp. nov.: Brazil: Bahia (MPEG 3762 from skin specimen MPEG 52345). *Cranioleuca pyrrhophia*: Bolivia: Santa Cruz (LSUMZ 125825). *C. albiceps*: Bolivia: La Paz (LSUMZ 101317). *Asthenes baeri*: Bolivia: Santa Cruz (LSUMZ 153909). *Asthenes dorbignyi*: Bolivia: La Paz (LSUMZ 101323). *Thripophaga fusciceps*: Bolivia: Beni (bill; LSUMZ 124064). *Phacellodomus sibilatrix*: Bolivia: Santa Cruz (LSUMZ 153910). *Xenerpestes singularis*: Peru: San Martín (bill; LSUMZ 84692). *Metopothrix aurantiacus*: Peru:

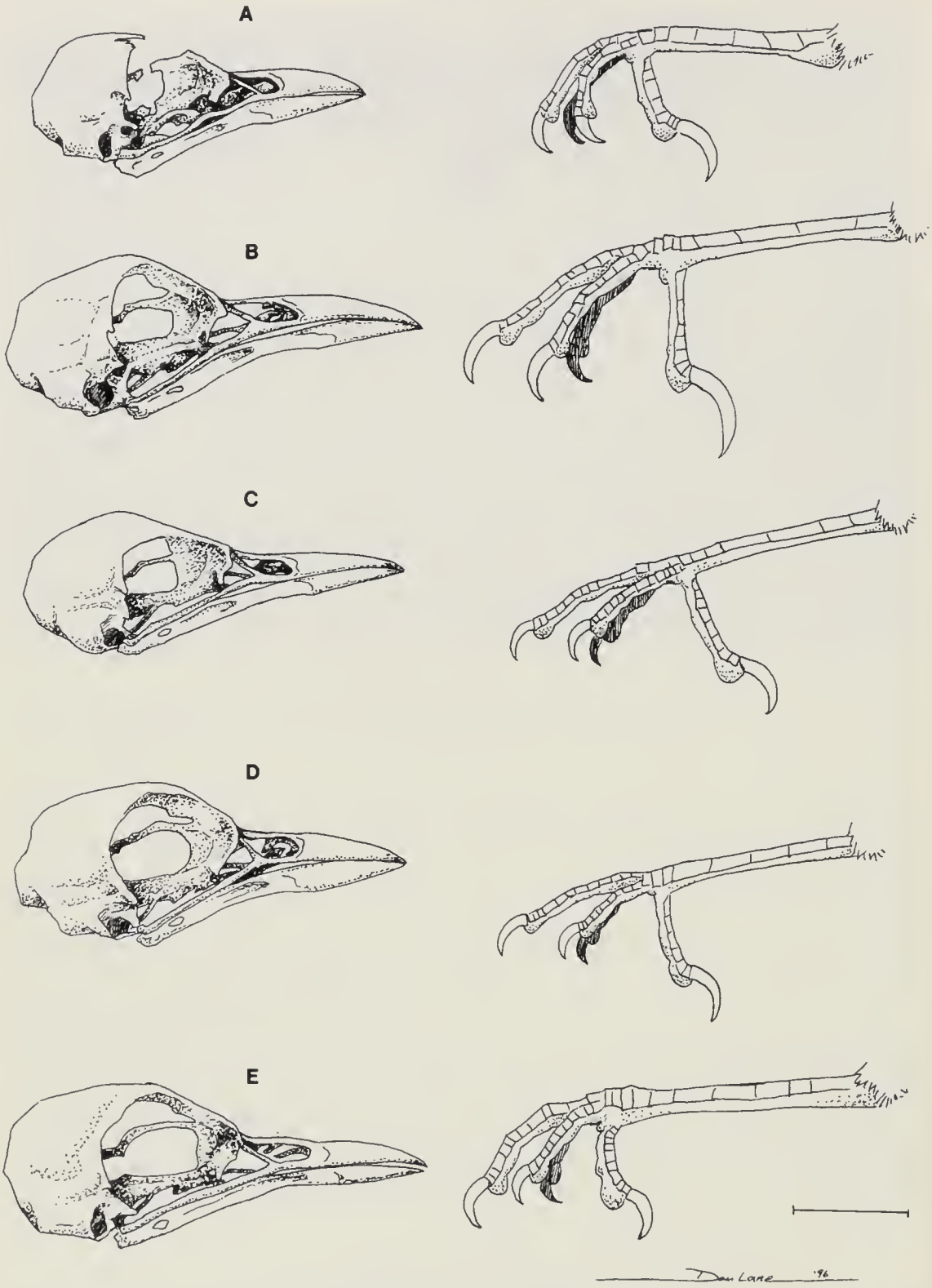

FIG. 2. Cranial and tarsal profiles of: A. *Acrobatornis fonsecai* gen. nov. sp. nov. (interorbital septum and frontal destroyed by shot); B. *Asthenes baeri*; C. *A. dorbignyi*; D. *Cranioleuca albiceps*; E. *C. pyrrhophia* to show the pseudo-schizorhinal skull of *Acrobatornis* and to permit general comparisons, especially bill shapes and relative thicknesses and lengths of tarsi, with some relevant taxa (continued).

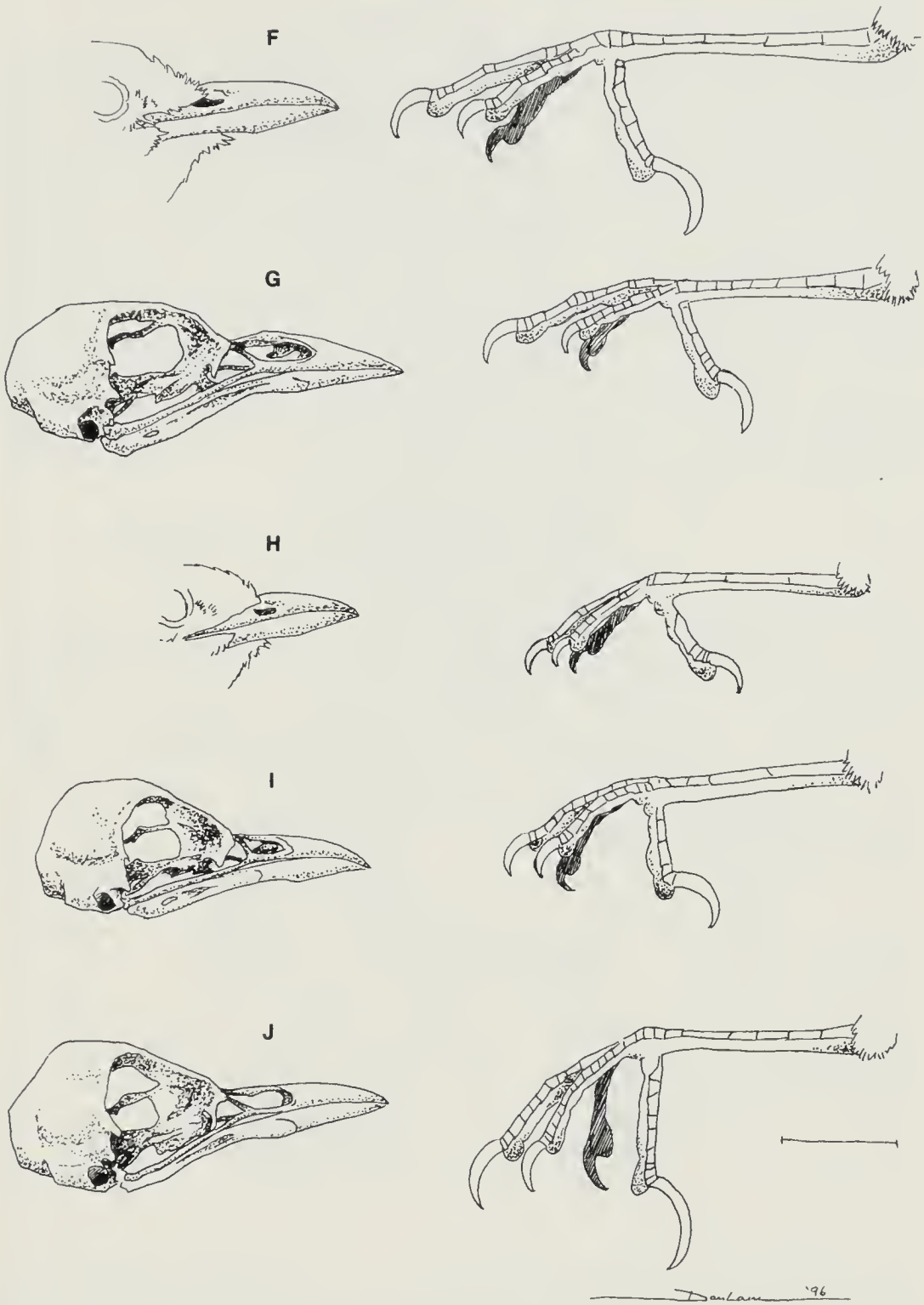

FIG. 2. (continued) Cranial and tarsal profiles of: F. *Thripophaga fusciceps* (no skull available); G. *Phacellodomus sibilatrix*; H. *Xenerpestes singularis* (no skull available); I. *Metopothrix aurantiacus*; J. *Margarornis squamiger* for comparison with *Acrobatornis fonsecai* gen. nov. sp. nov. in 2A. Drawings by Dan Lane.

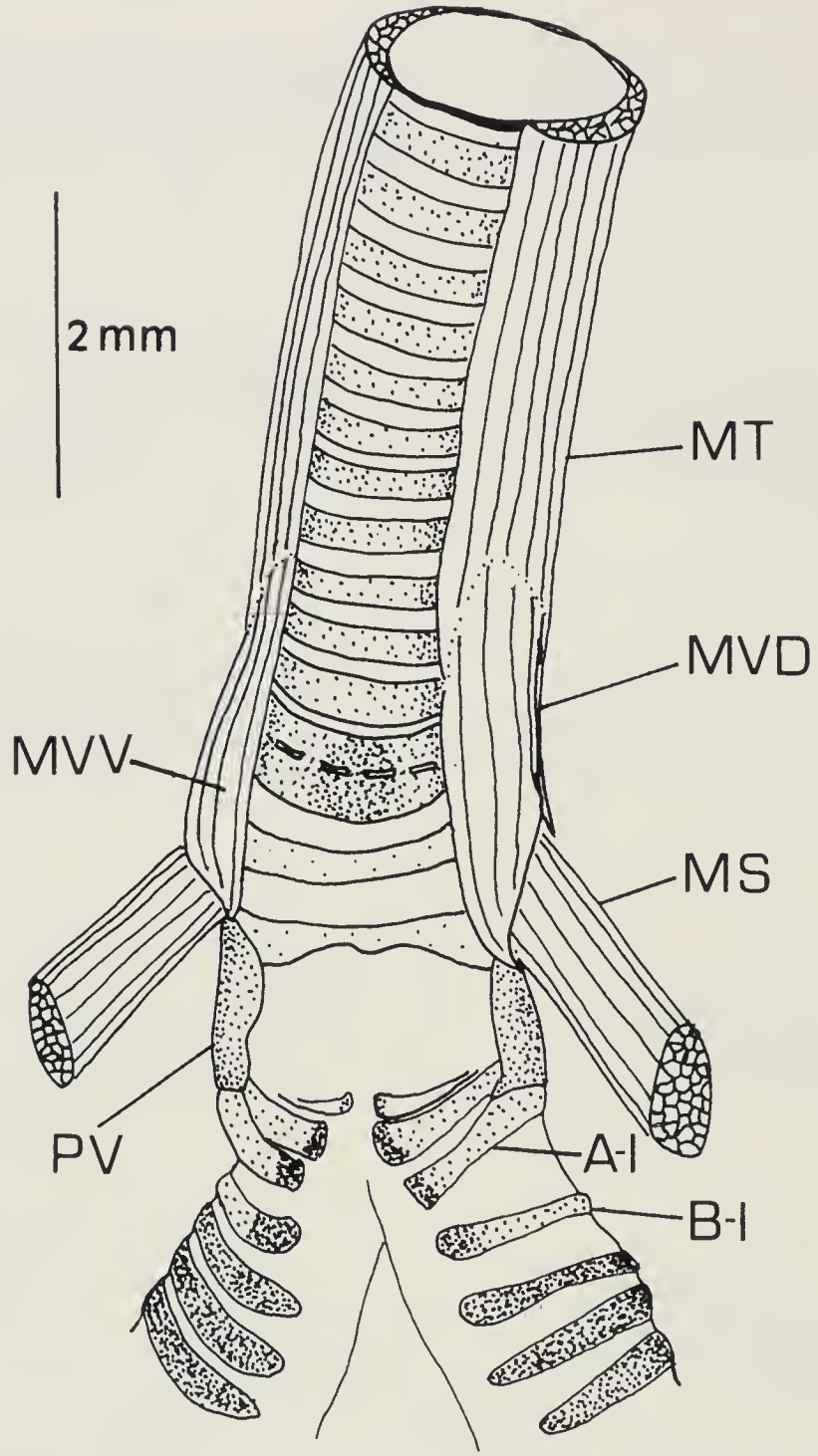

FIG. 3. Syrinx of *Acrobatornis fonsecai* gen. nov. sp. nov. showing well-defined Membranae tracheales and two pairs of intrinsic syringeal muscles, features that place it in the Furnarioidea. The lack of "horns" on the Processi vocales (PV) unequivocally places the new genus in the Furnariidae (as opposed to the Dendrocolaptidae). MT = M. tracheolateralis; MVD = M. vocalis dorsalis; MVV = M. vocalis ventralis; MS = M. sternotrachealis; PV = Processus vocalis; A-1 and B-1 = cartilaginous elements. Nomenclature follows Ames (1971). Drawing by Gonzaga.

Loreto (LSUMZ 51912). *Margarornis squamiger*: Peru: Pasco (LSUMZ 129867). Syrinx: *Acrobatornis fonsecai*: Brazil: Bahia (from holotype).

SPECIMENS EXAMINED: TAPE-RECORDINGS.—The voices of all but about 20 species of furnariids were included in initial comparisons with the vocalizations of *Acrobatornis* gen. nov. sp. nov. Selected recordings from which sound spectrograms were made are listed, with pertinent data, in the figure legends. All recordings will be archived at the Library of Natural Sounds (hereafter LNS), Cornell Laboratory of Ornithology, Ithaca, New York, and those made in Brazil, also at the Arquivo Sonoro Elias P. Coelho (ASEC), Universidade Federal do Rio de Janeiro, Rio de Janeiro.

BIOCHEMICAL SPECIMENS.—All biochemical specimens stored at LSUMZ, with the following tissue collection catalog numbers: B-26329 (voucher MZUSP 74154, holotype; male; blood); B-26330 (voucher MZUSP 74155; female; blood and liver in separate tubes); B-26331 (voucher MPEG 52345; male; blood and liver in separate tubes).

ETYMOLOGY.—From the Greek words *akróbatos,* and *órnis,* referring to the acrobatic climbing and hanging foraging behavior of this bird; the root *akróbatos* is immediately understood in a remarkably diverse set of languages. The name is masculine in gender.

Acrobatornis fonsecai sp. nov.
Pink-legged Graveteiro
Acrobata (Portuguese)

HOLOTYPE.—MZUSP No. 74154; adult male from 15°11′S, 39°23′W, at approximately 550m elevation in the serra das Lontras above Itatingui, Municipality of Arataca, Bahia, Brazil; 25 January 1995; collected by J. F. Pacheco, prepared by L. P. Gonzaga. Blood sample housed at LSUMZ, No. B-26329. Not tape-recorded.

DISTRIBUTION.—Apparently restricted to the region of southeastern Bahia between the drainage of the Rio de Contas in the north (known to just north of Ibirataia, 14°02′S, 39°40′W) and the Rio Jequitinhonha in the south (southernmost record near Teixeira do Progresso, approximately 15°45′S, 39°28′W), occurring west at least as far as Ipiaú (14°06′S, 39°42′W) and east as far as the vicinity of Itabuna (14°48′S, 39°17′W) (Fig. 4). Altitudinal distribution from near sea-level to approximately 550 m.

DESCRIPTION OF HOLOTYPE.—The two descriptive colors, "medium-gray" and "dark-gray," correspond to Munsell® Soil Color Chart (1994 ed.) 7.5YR 5/1 and 7.5YR 4/1, respectively. Crown black. Frontal and loral feathers (which are normal, not elongated or stiffened), posteriorly to approximately the anterior edges of the orbits, medium-gray with black apical margins imparting a grizzled appearance to these regions. Tiny feathers of malar and suborbital regions margined blackish more narrowly than the frontal feathers. Superciliary stripes subtly whiter, about 2.5 mm wide and 10 mm long posterior to orbit, blending into medium-gray of sides of neck. Post-ocular stripes (about 3.5 mm wide and 10 mm long) blackish and surrounded by medium-gray of headside. Nuchal and mantle feathers dark-gray with conspicuous blackish margins, imparting a weakly scalloped effect. Small, anteriormost scapular feathers largely blackish; larger, posterior ones wholly dark-gray. Middle back posteriorly through rump and upper tail coverts pure-medium-gray. Underparts from chin to belly same medium-gray as headsides, but appearing narrowly streaked (or mottled, on throat) with white, widest on lower breast, owing to white feather shafts and margins of these feathers. Medium-gray of flanks and undertail coverts very weakly tinged olivaceous, and streaking in these regions obsolete. Tail and wing in molt. Rectrices dark-gray, blackish at tips, lighter overall on undersurface; shafts blackish dorsally and whitish ventrally. Outermost rectrices with narrow but conspicuous whitish fringes on inner webs. Feathers at wrist whitish flecked with medium-gray. Alula and upper primary coverts black,

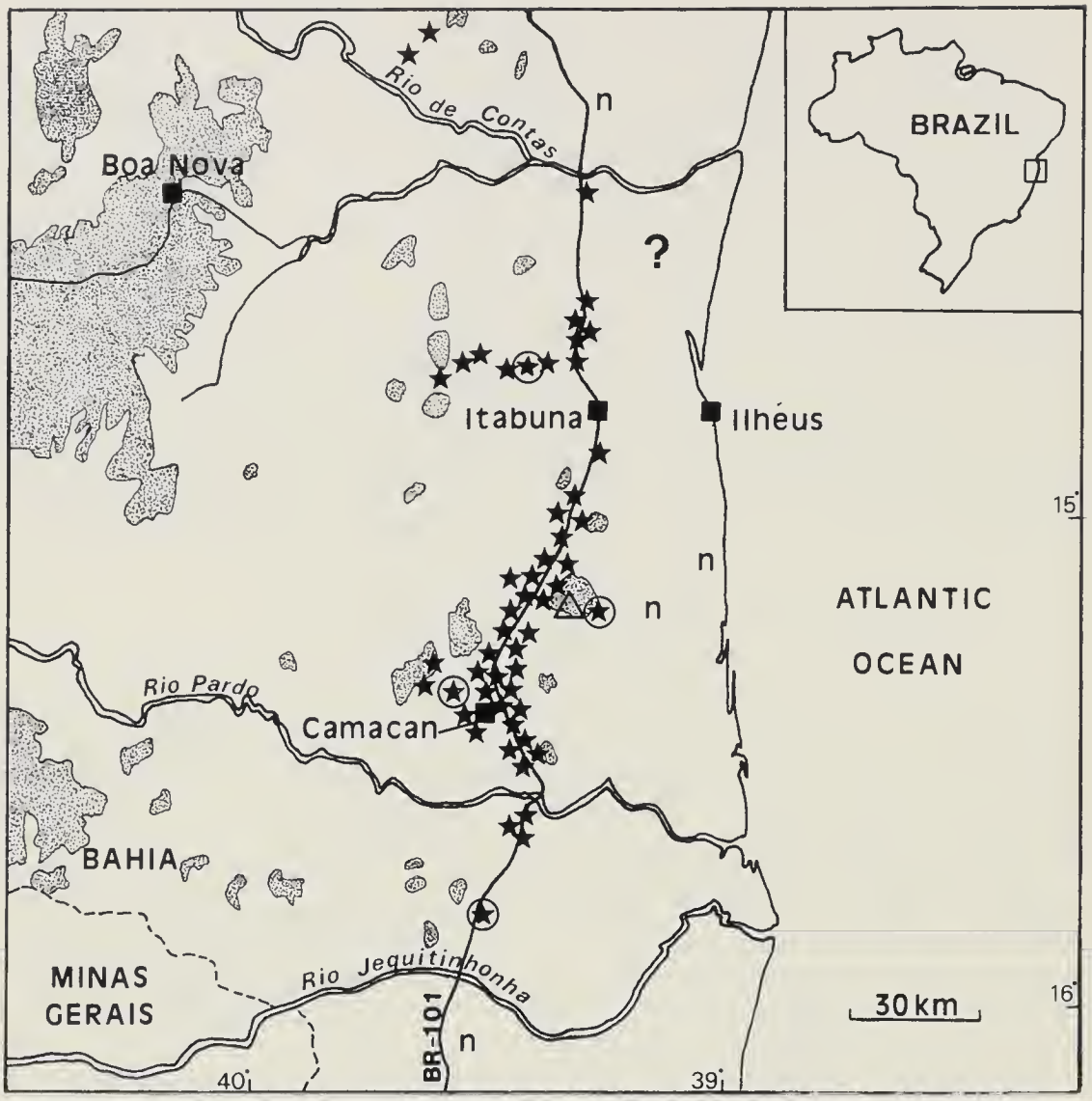

FIG. 4. Distribution of *Acrobatornis fonsecai* in southeastern Bahia, Brazil, showing principal rivers, cities, and the major highway BR-101. Triangle is the type locality in the serra das Lontras. Stars indicate trees with nests; a few sites very close together were mapped as a single point. Circled stars mark nests confirmed active in October 1995. The roughly linear distribution of stars reflects the fact that we conducted searches mostly from roadsides. "n" marks areas we searched for nests but found none. The single "?" is in a region we suspect holds *Acrobatornis* but which we were unable to check. Shaded areas are above 500 m elevation. Dotted line is the Bahia/Minas Gerais state boundary. We expect *Acrobatornis* occurs locally as far west as about 40°W, which is approximately the western limit of cocoa cultivation in this region.

forming a conspicuous, diagonally oriented slash along bend of folded wing; the other upper wing coverts black with light-gray or whitish borders producing, in effect, a gray-edged panel in the wing-covert region. Remiges blackish, narrowly margined (except two outermost pairs) light-gray on the proximal portion of outer webs (these margins widest where remiges meet the wing-coverts), and whitish on proximal one-half to two-thirds of inner

webs. Secondaries and tertials slightly paler than primaries, and similarly pale-fringed on outer webs; some worn feathers in this region, including at least one probable juvenal scapular feather with a brownish tinge. Soft parts in life: irides pale-gray; maxilla dark-brown; mandible pink; tarsi and feet clear, bright-pink; claws brownish-pink.

MEASUREMENTS OF HOLOTYPE (mm).—Wing (chord) 65.1; tail 56.0; culmen from base (at skull) 11.2; culmen from anterior edge nares 7.5; bill depth at anterior edge nares 3.6; bill width at anterior edge naes 3.0; tarsus 17.3; mass 15 gr.

DESCRIPTION OF FEMALE.—The single known female (MZUSP No. 74155) is like the holotype except mantle with almost no black, instead being concolor with the medium-gray back and rump. Wing with tips of primaries broken; tail 52.3; culmen from base (at skull) 11.6; culmen from anterior edge nares 7.5; bill depth not measurable; bill width at anterior edge nares 2.9; tarsus 17.2; mass unknown.

DESCRIPTION OF JUVENILE.—There are two specimens, both unsexed, quite similar in plumage, and patterned basically like the adults, but with gray regions instead largely reddish-yellow; MZUSP No. 74156 is described here. Frontal and supraloral feathers reddish-yellow (nearest 7.5YR 6/8; slightly oranger than Tawny, Color No. 38, of Smithe [1975]), a few, irregularly scattered ones, posteriorly to about the posterior edge of orbits, with conspicuous black tips or with thin black margins (possibly not juvenal feathers?). Crown feathers in orbital region slightly paler reddish-yellow, the pale shafts of which overlay darker, rather worn, brownish (7.5YR 4/2) feathers, producing a sublty streaked or mottled effect. Posterior half of crown more completely brownish, carrying a weak tinge of forecrown color. Superciliary stripes blending posteriorly into subtly darker sides of neck and nearly complete nuchal collar. Post-ocular stripes (perhaps extending anteriorly through loral region) slightly paler than crown, weakly contrasting with rather grizzled headsides. Mantle and scapulars pale-brownish (7.5YR 5/2), most washed with reddish-yellow, distinctly paler than crown, and with two or three medium-gray (7.5YR 5/1) feathers (probably not juvenal) in the anterior region. Rump and upper tail coverts rather bright yellowish-red (5YR 5/8). Underparts generally same reddish-yellow as sides of neck, but with a blotchy appearance owing to differences in color saturation of individual feathers (effects of wear?), grayish feather bases showing on some feathers, and small, pale, subapical spots on most throat feathers. There are also a few wholly gray feathers (probably not juvenal) on the side of the breast. Most rectrices are abraded at tips; central pairs slightly narrower than adult and not excised. The outermost three pairs largely orange-rufous (nearest 2.5YR 5/8), with this color concentrated on outer web. Dark-gray (7.5YR 4/1) bases present on all rectrices, increasing in extent from outermost to innermost such that three innermost pairs have largely dark proximal webs. Wing patterned as in adult (black regions same), but all gray feather margins instead yellowish-red (5YR 5/8). Secondaries and tertials with wider, more conspicuous margins, and primaries with thin, yellowish-red apical fringes instead of solidly blackish. Soft parts as in adults, with pale-grayish irides. Wing (chord) 61.1; tail 56.1; culmen from base (at skull) 11.3; culmen from anterior edge nares 7.2; bill depth not measurable; bill width at anterior edge nares 3.0; tarsus 17.3; mass 14 gr.

ETYMOLOGY.—We are pleased to name this distinctive new furnariid for Paulo Sérgio Moreira da Fonseca ("P.S.") of Rio de Janeiro, our multi-talented friend of many years, not only because he was the first to gasp in wonder at the living bird, but also in recognition of his unending encouragement and deep generosity. Through his excellence in the identification and observation of birds, P.S. has contributed much valuable data to our continuing studies of the Brazilian avifauna.

We designate the English name Pink-legged Graveteiro to call attention to conspicuous morphological and ecological features of the bird: the stout, bright-pink legs and feet, and the fact that it gathers twigs and sticks ("gravetos" in Portuguese) to construct its nest, as

do several other groups of furnariids, such as the canasteros ("basket-makers" in Spanish). Indeed, to call *Acrobatornis* a "canastero" or "thornbird" or "spinetail" or any other existing English name seems inappropriate, regardless of its phylogenetic affinities.

The Portuguese name Acrobata refers to the highly acrobatic foraging behavior of the new species, and this is the name we became accustomed to use while studying it in the field.

REMARKS

Variation in the type series.—The type series comprises four adults and two specimens in largely juvenal plumage. The adult specimens, aside from the holotype and the female described above, are an adult male (MPEG No. 52345), and an unsexed bird (LSUMZ No. 160000), both of which are virtually like the holotype except that they have considerably less black feather-edging in the mantle region, more closely approaching the adult female than the holotype. The second juvenile specimen, MPEG No. 52346, is very much like MZUSP No. 74156, but with all orangish feathers slightly paler, and with the lower back and rump largely medium-gray. This specimen weighed only 12 g.

Habitat.—Mori (1989) summarized specific climatic data from the lowland "moist forest" of southeastern Bahia, and characterized the region as generally hot and humid, without a distinct dry season (but with short, unpredictable dry periods of one to three months), and with rainfall greater than 1300 mm/year. *Acrobatornis fonsecai* inhabits the canopy and subcanopy in a restricted section (Fig. 4) of the moist Atlantic Forest domain of southeastern Bahia, hereafter referred to as the Itabuna-Camacan region. Native forest within its known range, where not removed altogether, has been converted to cocoa (*Theobroma cacao*) plantations virtually completely; we found no intact forest habitat below about 400 m elevation and almost none below 600 m. Traditionally, cocoa is cultivated by thorough removal of the native forest understory, and thinning of the canopy to about 25 trees/hectare to provide the necessary shade for the growing cocoa, a system known as "cabruca" (Mori et al. 1983). Within the known range of *Acrobatornis,* cocoa is cultivated to elevations of about 600 m (pers. observ.); indeed, there is little land above this elevation. We found *Acrobatornis fonsecai* only in canopy trees left to shade cocoa plantations (Fig. 5).

When first discovered at 550 m in the serra das Lontras (which turned out to be the highest elevation at which we ever found it), we expected that *Acrobatornis* was a montane forest species, like other undescribed forms recently discovered in southern Bahia. It soon became apparent, however, that *Acrobatornis* was absent from undisturbed montane forest and, at these higher elevations, was to be found only in the tall trees shading cocoa, beyond the forest edge. Following our October field ex-

FIG. 5. Habitat of *Acrobatornis fonsecai* gen. nov. sp. nov. *Leguminosae* and other trees (thinned, "cabruca" canopy) shading cocoa monoculture at the type locality in the serra das Lontras of southeastern Bahia, Brazil. Three nests of *Acrobatornis* are visible in the canopy of the thin tree right of center (two nests above the horizon, one below). Photo by Whitney.

pedition, all evidence indicates that *Acrobatornis* has spread from a narrow distributional center in the contiguous lowlands into the higher elevations of the serra das Lontras and serra Bonita, exactly following the opening of these denser, more humid, montane canopies for the propagation of cocoa.

The broken, cabruca canopies in the Itabuna-Camacan region, and the continuous canopies of undisturbed forests above about 500 m, have many trees heavily laden with bromeliads, lianas, orchids, and mosses. We also noted many species and individuals of Leguminosae (e.g., *Ery-*

thrina verna, Senna multijuga, Schizolobium parahyba, Inga spp.), the small leaves and relatively open canopies of which allow much greater penetration of sunlight and wind and, consequently, support almost no epiphytic growth. *Acrobatornis* favors Leguminosae for nesting (Whitney et al. 1996). Other species of Leguminosae listed by Lewis (1987) as common in the cocoa-growing region of southern Bahia are *Diplotropis incexis, Platycyamus regnellii, Sweetia fruticosa, Parkia pendula,* and *Plathymenia foliolosa.* In late January, *Acrobatornis* also foraged in large, flowering, *Croton* sp. trees (Euphorbiaceae; see frontispiece).

The native habitats of the Itabuna-Camacan region have suffered extensive alteration for so long that it is now difficult, perhaps impossible, to reconstruct the natural habitats there beyond a basic structural description. What is clear is that *Acrobatornis* has been able to tolerate radical changes in the habitat in which it evolved, in both a paleoclimatic timeframe, over probably millions of years, and a recent-historical context, over the past century or so. Today, *Acrobatornis* persists as a fairly common species along roads, including even the major Brazilian highway, BR-101 (we have even observed it flying across this thoroughfare), and forages and nests in close proximity to human presence (see Fig. 10 in "Conservation," below).

We suspect that *Acrobatornis* is absent from coastal forests east and south of Itabuna, where recent, pluviomarine soils (RADAMBRASIL 1981; see discussion under "Origins" below) and forest structure (pers. observ., unquantified) differ from those in the Itabuna-Camacan region. We failed to find *Acrobatornis* along the principal roads from just east of Arataca east to Una (practically on the coast), then north along the coast to near Ilheus. Indeed, we noted few cocoa plantations east of the vicinity of Arataca (which might reflect the different soil type?). We did not conduct tape-playback presentations to attempt to find birds, but base the above suggestion on the fact that we noted no nests of *Acrobatornis* (see below). *Acrobatornis* might occur somewhat farther east, to the north of Ilheus, where soils and cocoa plantations quite near the coast are apparently much like those in the Itabuna-Camacan region; we did not have an opportunity to explore this area (see "?" in Fig. 4). We expect it occurs west to about 40°W, which is near the western limit of cocoa cultivation in this region.

Breeding.—As appears to be true of most species of passerines in the Atlantic Forest (pers. observ.), *Acrobatornis* breeds in the September/October, spring period, at least. Two adults collected in early October appeared to be in breeding condition and, at this season, the birds were singing conspicuously and feeding both nestlings and fledged, food-begging juveniles. On 4 October 1995, when we were actively looking for

potential nests of the new species, it was the food-begging calls of nestling *Acrobatornis* that first called our attention to an unusually sized and shaped stick-nest in the canopy of a leafy *Erythrina* tree. Nests were characteristic, often conspicuous masses of sticks and twigs in the canopies of tall trees, easily seen from roadsides. We confirmed that the presence of nests was a highly reliable indicator of the presence of *Acrobatornis*, as previously undetected birds responded within 1 min to playback of tape-recordings presented below nests. The nest and nesting ecology of *Acrobatornis fonsecai*, and implications for intrafamilial relationships, were described by Whitney et al. (1996).

We observed adult *Acrobatornis* feeding young in four nests at widely scattered localities (Fig. 4). At one active nest, we determined that both adults feed the young, although they usually were not at the nest simultaneously. Feeding intervals between 08:30 and 11:00 averaged about once every 10 min., with more regular feedings earlier in the period. Feeding intervals probably vary considerably with the age of the young; noisiness of the young in this nest suggested that they were fairly well-developed. We also noted that adults (perhaps only the male?) usually sang once from near the nest entrance immediately after feeding the young. At another active nest in which no young birds were audible, we suspect that the adult (presumed female, as the presumed male was singing some 50 m away at the time) was incubating or brooding small young, because it once stayed inside the nest for 13 mins. We suspect that the clutch size is two or three, because we saw pairs of adults accompanied by two young birds several times and, on two occasions, by three presumed offspring (one of which could have been from a previous nesting). Gonads of the two adult specimens collected in late January were largely destroyed by shot (one could not be sexed), such that reproductive condition was not possible to determine, but Pacheco, Fonseca, and Bauer noted that *Acrobatornis* was not vocal and was generally inconspicuous then. Similarly, Whitney noted relatively poor response to tape playback in early March, and presumed young birds in the company of adults were not food-begging.

Molt.—Of the two (adult) specimens of *Acrobatornis* collected in early October, during the breeding season, one (female) showed no sign of molt, and one (male) was molting the inner primaries; tail molt had not commenced. The two adults collected in late January had little evidence of molt in the head and body. One (male; holotype) was molting primary No. 7 and molt of the rectrices was well underway. It had retained at least one brownish-tinged scapular feather on the left side. The other specimen (unsexed) was molting some primaries but no rectrices. Juvenal plumage is apparently replaced in the postjuvenal molt. Both juveniles

collected in late January showed at least one ingrowing, adult-colored rectrix and several black or gray head and body feathers. If these birds were fledged in the previous breeding season, definitive feathering is probably attained by about six months age. Although we have no firm evidence that *Acrobatornis* has a distinct subadult plumage (one ingrowing rectrix with a rufous margin on the right side of MZUSP No. 74156 seems different from adult), as do *Scytalopus* tapaculos, for instance, this merits further attention.

Behavior and ecology.—Acrobatornis fonsecai foraged in the canopy and subcanopy of tall trees, virtually always in the company of mixed-species flocks of small insectivores and frugivores. Consistent flock associates in cocoa plantations were Gray Elaenia (*Myiopagis caniceps*), Chestnut-crowned Becard (*Pachyramphus castaneus*), Black-capped Becard (*P. marginatus*), Streaked Xenops (*Xenops rutilans*), Rufous-browed Peppershrike (*Cyclarhis gujanensis*), Red-eyed Vireo (*Vireo olivaceus*); Tropical Parula (*Parula pitiayumi*), Bananaquit (*Coereba flaveola*), Flame-crested Tanager (*Tachyphonus cristatus*), Sayaca Tanager (*Thraupis sayaca*), Palm Tanager (*T. palmarum*), Violaceous Euphonia (*Euphonia violacea*), Chestnut-bellied Euphonia (*E. pectoralis*), Green-headed Tanager (*Tangara seledon*), Red-necked Tanager (*T. cyanocephala*), and Blue Dacnis (*Dacnis cayana*). At higher elevations, Rufous-headed Tanager (*Hemithraupis ruficapilla*) was a near-constant member of mixed-species flocks, and a variety of other species occasionally joined near undisturbed forest borders. At about 550 m in the serra das Lontras, *Cranioleuca pallida* (Pallid Spinetail) foraged in some of the same mixed-species flocks as *Acrobatornis,* generally keeping to lower heights and in more tangled vegetation, performing gleans and short reaches in vines and dead leaves, but also gleaning from bark.

Acrobatornis traveled through the treetops with a variety of acrobatic maneuvers, seldom spending more than about 10 sec. at a foraging site. The birds also flew strongly, adults sometimes traversing more than 300 m in a single flight to join mixed-species foraging flocks after feeding young at the nest. The most characteristic foraging maneuvers were inverted hangs and inverted creeping or hitching along limbs (ranging in diameter from about 3 mm to 8 cm), with the tail parallel to the substrate; we estimated these behaviors constituted at least 80% of search maneuvers (terminology follows Remsen and Robinson 1990). Most other searches were scansorial along the uppersides of limbs. Individuals crawled with agility over and through the terminal leaf- and flower-clusters of tall trees, hanging and swinging as they poked their heads into the foliage. Their powerful legs and feet (Fig. 2A) allowed them to perform these maneuvers without fluttering the wings for balance. Unfortunately,

we were not able to determine the precise orientation of the legs and feet during scansorial locomotion, but some of these behaviors were videotaped, and might show sufficient detail to be informative in future study. Almost all attack maneuvers were near-perch, mostly gleans in live foliage and flowers, and probes in moss coating trunks and limbs and the bark of dead limbs. They also reached into new, unopened (still curled) leaves, probing deeply with the bill. On only one occasion did we note dead-leaf searching. An adult *Acrobatornis* hitched along terminal branchlets to reach a small cluster of dead leaves, then poked and probed in these for several seconds. Most of the trees in which *Acrobatornis* foraged (Leguminosae) did not hold dead leaves or leaf-clusters, and their tall canopies trapped few dead leaves fallen from other trees.

On two occasions (one of which was partially video-taped) we observed *Acrobatornis* hitching upwards for distances of about 1 m on the principal trunks of trees at least 25 cm in diameter at foraging height (about 20 m above ground), using the tail as a brace or prop (a behavior rarely reported in Furnariidae), and probing intently in moss and at the bases of small epiphytic ferns and a bromeliad (spending nearly 3 min at this latter site). In general, trees in which *Acrobatornis* foraged held (apart from thin patches of moss) almost no epiphytic growth.

On the afternoon of 11 October, following a brief but hard rain, we observed a family group of *Acrobatornis* foraging in the mostly leafless canopy of a tree at least 35 m tall. One adult performed two aerial, flycatching maneuvers to capture large, winged termites. It flew about 3 m upwards from the crown of the tree, stalled as it took the insect in the bill, then fluttered back to land near the other birds. Each time, a food-begging juvenile followed the adult after it landed, but was not fed. Instead, the adult bounded away quickly through the branches, and once we were able to see it hold the termite with its foot as it pecked it against the limb and swallowed it.

Apparently, most prey were very small; the only items we were able to see clearly in the field were the winged termites, several small caterpillars (fed to nestlings and food-begging juveniles), and a fairly large moth (gleaned from a dead limb) that fluttered in the bird's grasp for several seconds before being subdued and swallowed. Stomachs of three specimens collected in January contained remains of tiny arthropods. These were principally Coleoptera (including several Curculionidae and one Staphylinidae), which were present in all stomachs and represented 58% of all (N = 90) identifiable food items. Ants and insect larvae (including catterpilars) were also present in all stomachs, but the first totaled only 11% and the latter only 7% of the items. Other insects included winged Hymenoptera (including a minute apoid), Hemiptera, and Ho-

moptera (including two nymphs). Insect eggs, oothecae of an orthopteroid, and spiders were also found, each in only one of the stomachs examined.

Singing posture was nearly vertical, with the bill parallel to the ground and opened fairly widely. Sometimes, as the birds sang, they leaned forward and swung the head and neck from side to side, broadcasting the song more widely. In response to tape playback of songs in October, individuals (often just the presumed male) usually responded almost immediately by flying in to perch in the tree nearest the tape recorder. They perched in an upright posture and remained silent for up to several minutes. They then either sang one song before departing or, most frequently, flew off to rejoin the female and sang once from there. With repeated tape playbacks, males twice descended to near the ground, and females and immatures sometimes came to trees overhead.

Vocalizations.—The vocal repertoire of *Acrobatornis fonsecai* is typical of that of most furnariids (pers. observ.). Whitney recorded 29 songs (at least 19 of which were in response to playback) from 12–14 individual adult *Acrobatornis,* and other vocalizations from several (number undetermined) individuals, four of which were immatures or juveniles. The natural (unsolicited) song may be generally characterized as a simple series of very short, piercing syllables at about 5.5 kHz that begins with syllables delivered slowly enough to be counted (5–8/sec), then gradually accelerates in pace while decreasing slightly in amplitude, finishing with syllables spaced tightly. It is almost always introduced by 2–4 more irregularly spaced, sharp syllables, and lasts from about 4–8 sec (Fig. 6A, B, C). Some parameters of songs vary slightly, mostly with respect to overall duration. The shortest songs always begin as described above, but then do not achieve a delivery rate greater than about 15 syllables/sec. Longer songs, and those given in response to playback, finish with syllables delivered at a rate of 20–26/sec, and the series tends to drop approximately 0.5 kHz in frequency as it loses amplitude (Fig. 6B, C). Songs given in response to playback may be nearly 12 sec in duration and usually have a few stutters in the fastest section, after the halfway point (Fig. 6C). Songs are audible to at least 200 m. *Acrobatornis* produces a duet in which the two members of the pair sing different parts. The presumed male sings a normal version of the song and the female joins in with irregularly paced bursts of sharp chips much like the introductory syllables of songs (Fig. 6D). Few duets were heard, and these were in response to tape playback.

Calls given by foraging *Acrobatornis* are short, sharp, single syllables delivered at irregular intervals; flight calls are similar. Food-begging juveniles utter a slightly higher-sounding version of this call and sometimes

give doublets with the two elements about 0.17 sec apart and the first slightly louder (adult and juv. calls Fig. 6E). Also given by adults, although rather rarely (heard only twice), is a chattery vocalization that may be a pair greeting. It is delivered when one member of a pair that has been foraging apart flies in to land near its mate. It may be described as a jumble of 10–12 syllables, quietest in the middle, then loudest through the final three or four syllables, which are more distinctly separated from each other (Fig. 6F). Complete songs are sometimes delivered immediately following this vocalization. We did not hear the scolding or mobbing vocalization of *Acrobatornis*.

SYSTEMATIC RELATIONSHIPS, ORIGIN, AND DESTINY

Phylogeny and classification of the Dendrocolaptidae/Furnariidae complex, or of its many subgroups, have been the subjects of some important recent studies (Vaurie 1971, 1980; Feduccia 1973; Sibley and Ahlquist 1985; Rudge and Raikow 1992a,b; Clench 1995), all of which, however, have focused on morphological comparison with limited or inconsistent discussion of other characters. Vaurie (1980) focused especially on nest location and architecture. Owing to the variety of taxa judged "intermediate" in one or another kind of analysis, and the fact that many species and several genera have not been included in most of these analyses, even familial limits remain the subject of considerable debate. Detailed documentation of a new genus, then, especially one well-differentiated from all others and perhaps basal to some contemporary groups, seems particularly desirable. Placement of the new genus in the Furnariidae requires comparison to several other, possibly related genera. Much further analysis, incorporating morphological, vocal, ecological, and biochemical data (a great deal of which are now available) is needed to construct a well-corroborated phylogeny of this large and complex assemblage of birds.

In Table 1 (comparative mensural data from selected furnariids), Fig. 2 (skulls and tarsi), and Figs. 6–9 (spectrograms of songs and other vocalizations; many examples from near type localities), we present comparative data for *Acrobatornis* and a variety of selected genera (and selected species of each) that we judge, from field and museum experience, to be relevant, regardless of degree of actual relatedness. These are: *Cranioleuca, Asthenes, Thripophaga, Phacellodomus, Xenerpestes, Metopothrix,* and *Margarornis*; aspects of each will be described and discussed relative to *Acrobatornis*. We consider each of them, except *Asthenes,* to be monophyletic as currently defined, or close enough to monophyletic (e.g., *Cranioleuca*) for the purposes of the present comparisons. Perhaps the monotypic *Siptornis* should be considered as well, but we have insufficient data (no nest, no recordings of song). Tails of these various

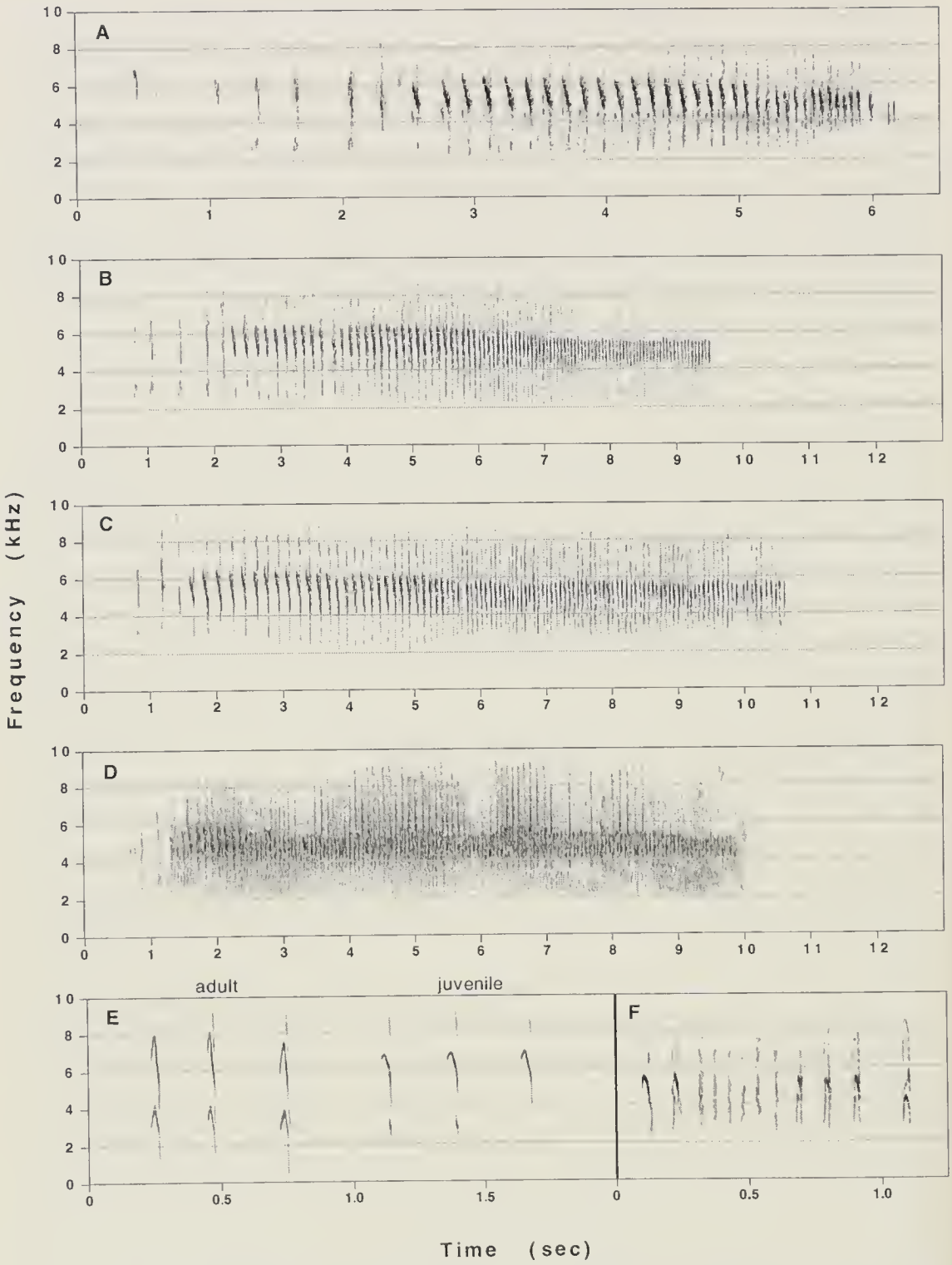

FIG. 6. Sound spectrograms of vocalizations of *Acrobatornis fonsecai* gen. nov. sp. nov. for comparison with those of other taxa shown in subsequent figures. All songs in this and subsequent figures (except A in this figure) shown on same time scale; all other vocalizations are on a scale 4× that of songs to show greater detail. A. Natural song, short version, presented on scale 2× that of other songs. Serra das Lontras, 5 Oct. 1995, 475 m. B. Natural song, long version, with more rapidly paced ending. Serra das Lontras, 8 Oct. 1995, 480 m.

genera are at least moderately graduated and composed of 12 rectrices that are somewhat stiffened, except *Thripophaga* and *Xenerpestes,* in which rectrices are soft. Most of the following discussion of these genera stems from Whitney's unpublished observations.

Cranioleuca.—Bill length varies substantially in *Cranioleuca* (e.g., Fig. 2B, C), with even the smallest-billed species (such as *C. curtata* Ash-browed Spinetail) considerably longer-billed than *Acrobatornis* (Table 1). Body mass is roughly similar (Table 1). Tail/wing ratios for the three representatives of *Cranioleuca* in Table 1 average 1.1 (and all species have the tail longer than the wing, although the *albiceps* complex has low tail/wing ratio), whereas *Acrobatornis* has the tail shorter than the wing with an average ratio of 0.89. Rectrices of almost all *Cranioleuca* species are acuminate and, in many species, the innermost are excised on the inner web near the tip, forming a point without an exposed spine. The excised tips of the rectrices of some *Cranioleuca* taxa closely approach the shape of those of *Acrobatornis.* Wings and tails of all members of *Cranioleuca* are almost entirely rufous, but many species show darker feathers in the alula region, and some have blackish proximal webs on the primary coverts. The obvious difference in color aside, none shows as marked a pattern, or the same pattern, on the wing as *Acrobatornis,* but we do see a vague similarity. Almost all species of *Cranioleuca* have pale superciliary stripes contrasting with a dark (brown or rufous, streaked in two) crown or cap; a few have dark superciliaries contrasting with buffy or white crowns. The superciliaried/capped pattern of *Cranioleuca* seems much like that of *Acrobatornis,* but this pattern is pervasive in Furnariidae. All members of *Cranioleuca,* except the marsh-inhabiting *C. sulphurifera* (Sulphur-bearded Spinetail), forage arboreally and almost exclusively with mixed-species flocks, moving through the middle strata and subcanopies (*C. albiceps* complex in understory) of forest and woodland with short hops and hitches along horizontal and vertical substrates, performing reaches and gleans from vines, bark, dead leaves, and tangles,

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C. Song after tape playback of conspecific song, which is essentially identical to the long natural song shown in B. 7 km W Camacan, 12 Oct. 1995, 105 m. D. Duet in which one bird (adult male?) delivers a long song and is joined by the other bird giving irregularly paced bursts of similar syllables. Serra das Lontras, 7 Oct. 1995, 475 m. E. Calls: foraging/contact of adult (three on left) and food-solicitation of one accompanying juvenile (three on right). 4 km W Arataca, 11 Oct. 1995, 110 m. F. Chatter that seems to serve as a pair greeting call, and is sometimes followed immediately by the song. Same loc. and date as E. All recordings by Whitney. Sound spectrograms produced with "Canary" 1.2 of the Bioacoustics Research Program of the Cornell Laboratory of Ornithology, Ithaca, New York, and "Canvas" of Deneba Software, Miami, Florida.

TABLE 1
STANDARD MEASUREMENTS OF *ACROBATORNIS FONSECAI* AND SELECTED OTHER GENERA AND SPECIES OF FURNARIIDAE

	Acrobatornis fonsecai	*Asthenes*		*Cranioleuca*			*Thripophaga fusciceps*	*Phacellodomus sibilatrix*	*Xenerpestes singularis*	*Metapothrix auranticacus*	*Margarornis squamiger*
		baeri	*dorbignyi*	*albiceps*	*pyrrhophia*	*curtata*					
Bill width x̄ ± SD (N) range	3.0 ± 0.05 (4) 2.9-3.0	3.0 ± 0.38 (5) 2.6-3.6	3.0 ± 0.13 (4) 2.9-3.2	3.2 ± 0.06 (3) 3.2-3.3	2.8 ± 0.21 (3) 2.6-3.0	3.3 ± 0.29 (4) 3.0-3.7	4.1 ± 0.10 (3) 4.0-4.2	3.3 ± 0.33 (4) 3.0-3.8	3.2 ± 0.18 (5) 3.0-3.4	3.2 ± 0.06 (3) 3.1-3.2	3.1 ± 0.15 (3) 3.0-3.3
Bill depth x̄ ± SD (N) range	3.6 ± 0.07 (2) 3.5-3.6	3.5 ± 0.24 (4) 3.4-3.9	3.7 ± 0.26 (4) 3.5-4.0	3.9 ± 0.10 (3) 3.8-4.0	3.4 ± 0.06 (3) 3.4-3.5	3.7 ± 0.26 (4) 3.5-4.1	4.7 ± 0.15 (3) 4.5-4.8	3.9 ± 0.14 (2) 3.8, 4.0	3.3 ± 0.15 (5) 3.1-3.5	3.3 ± 0.07 (2) 3.3, 3.4	3.3 ± 0.0 (3) 3.3-3.3
Bill length from nares x̄ ± SD (N) range	7.4 ± 0.16 (4) 7.2-7.5	7.6 ± 0.48 (5) 6.9-8.1	9.9 ± 0.25 (4) 9.6-10.2	10.2 ± 0.15 (3) 10.0-10.3	10.5 ± 0.55 (3) 9.9-10.9	9.5 ± 0.88 (4) 8.9-10.8	10.0 ± 0.17 (3) 9.9-10.2	8.5 ± 0.61 (4) 8.1-9.4	7.7 ± 0.57 (5) 6.8-8.3	8.1 ± 0.20 (3) 7.9-8.3	7.9 ± 0.10 (3) 7.8-8.0
Bill length from skull x̄ ± SD (N) range	11.4 ± 0.21 (4) 11.2-11.6	12.2 ± 0.52 (5) 11.8-13.1	15.4 ± 0.32 (4) 15.1-15.8	13.9 ± 0.29 (3) 14.9-15.1	16.2 ± 0.42 (3) 15.7-16.5	15.1 ± 1.09 (4) 14.4-16.7	15.6 ± 0.32 (3) 15.4-16.0	13.5 ± 0.84 (4) 12.8-14.7	11.5 ± 0.51 (5) 10.9-12.1	11.7 ± 0.06 (3) 11.6-11.7	13.9 ± 0.29 (3) 13.6-14.1
Tarsus x̄ ± SD (N) range	17.5 ± 0.42 (5) 17.2-18.2	19.7 ± 1.09 (4) 18.5-21.0	24.4 ± 0.14 (4) 24.2-24.5	20.3 ± 0.21 (3) 20.1-20.5	19.7 ± 1.08 (3) 18.9-20.9	18.8 ± 0.55 (3) 18.3-19.4	21.8 ± 0.15 (3) 21.6-21.9	18.5 ± 0.17 (3) 18.4-18.7	15.5 ± 0.12 (3) 15.4-15.6	15.0 ± 0.21 (3) 14.8-15.2	20.5 ± 0.66 (3) 20.1-21.3
Tail x̄ ± SD (N) range	55.4 ± 2.10 (5) 52.3-58.0	62.9 ± 5.58 (5) 56.5-70.4	74.6 ± 1.91 (4) 72.2-76.2	65.2 ± 0.87 (3) 64.5-66.5	75.6 ± 0.42 (3) 75.3-76.1	73.4 ± 4.33 (3) 70.2-78.3	87.4 ± 3.75 (2) 84.8, 90.1	62.4 ± 1.82 (4) 59.7-63.6	49.1 ± 1.25 (4) 48.4-51.0	51.5 ± 1.21 (3) 50.1-52.2	72.3 ± 1.42 (3) 70.8-73.6
Wing x̄ ± SD (N) range	63.6 ± 3.54 (4) 60.2-67.8	58.1 ± 3.59 (5) 55.3-62.1	67.1 ± 4.22 (4) 62.6-71.4	64.9 ± 0.80 (3) 64.2-65.8	64.6 ± 2.40 (3) 61.9-66.4	65.7 ± 1.57 (4) 64.0-67.2	74.4 ± 3.70 (3) 70.1-76.7	55.8 ± 1.35 (4) 54.7-57.5	55.9 ± 1.51 (5) 54.0-57.8	57.9 ± 0.58 (3) 57.5-58.6	76.2 ± 1.15 (3) 75.3-77.5
Mass x̄ ± SD (N) range	13.7 ± 1.26 (4) 12.0-15.0	14.4 ± 0.55 (3) 14.0-15.0	18.4 ± 0.48 (4) 18.0-19.0	15.7 ± 1.05 (3) 14.6-16.7	12.9 ± 0.72 (3) 12.1-13.5	16.7 ± 1.06 (2) 16.0; 17.5	25.2 ± 1.04 (3) 24.0-25.9	15.6 ± 0.61 (3) 14.9-16.0	11.6 ± 0.48 (4) 11.0-12.0	11.3 ± 0.21 (2) 11.2, 11.5	16.2 ± 2.07 (3) 14.5-18.5

and probes in mosses and epiphytic growth. *Cranioleuca* spinetails rarely hang inverted for more than 1–2 sec. There are some published reports of scansorial foraging in *Cranioleuca* (e.g., Skutch 1969, Vuilleumier note 81 *in* Vaurie 1980), and we have observed this behavior ourselves many times. We do not believe that any member of *Cranioleuca* is as highly scansorial, or hangs as much, as *Acrobatornis,* which we suspect is reflected in the relatively short and stout tarsus of *Acrobatornis* (compare Fig. 2A with 2D, E).

Cranioleuca shows remarkable homogeneity in vocalizations across its 18 or so members, especially the montane and far-southern species, which is most of them. These songs are short (generally less than 2 sec) series of thin, spritely, syllables on a level or slightly descending frequency (the last syllable or two almost always at lower frequency), introduced by two or three relatively loud and widely spaced syllables with subsequent syllables spaced more closely and quieter (Fig. 7A, B; two species selected from recordings of all species). *Cranioleuca* songs of this type, except for their relatively rapid beginning and truncated length, are structured much like and sound similar to the song of *Acrobatornis.* Songs of *C. gutturata* (Speckled Spinetail) and the two or three members of the *C. vulpina* (Rusty-backed Spinetail) complex, all principally of lowland Amazonian distribution in river-created habitats, differ distinctly from those of the other members of the genus (and from each other) and do not approach the song of *Acrobatornis. Cranioleuca* calls are short, sharp,

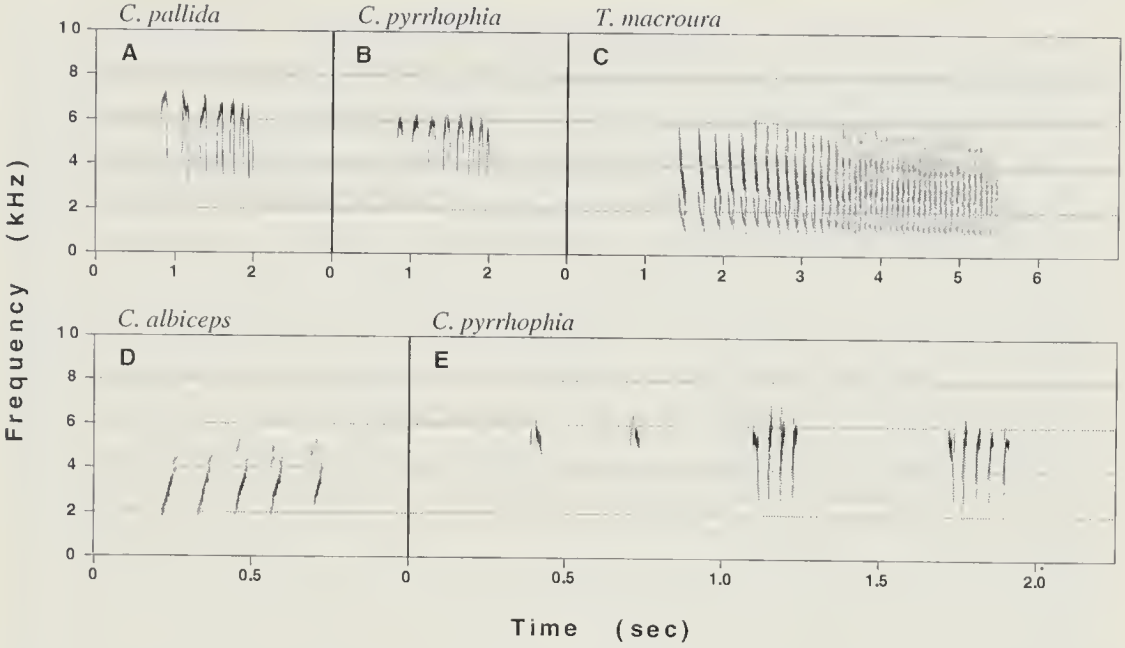

FIG. 7. Sound spectrograms of vocalizations of selected *Cranioleuca* species and *Thripophaga macroura.* A. *Cranioleuca pallida,* natural song. Brazil: Bahia, about 10 km E. Boa Nova, 8 Aug. 1993, 900 m. Recording by Gonzaga. B. *C. pyrrhophia,* natural song. Argentina: Salta, about 75 km E. J. V. Gonzalez, 30 Dec. 1987, 330 m. Close resemblance in species shown in A and B is characteristic of the montane and far-southern members of the genus (thus, most species). C. *Thripophaga macroura,* natural song. Bahia, near Almadina, 9 Oct. 1995, 425 m. D. *Cranioleuca albiceps,* scold. Bolivia: La Paz, 31 Mar. 1993, 3180 m. E. *C. pyrrhophia,* calls (two on left) and scold (two series on right). Argentina: Salta, about 60 km E. J. V. Gonzalez, 29 Dec. 1987, 330 m. LNS 43819. Scolds of most *Cranioleuca* species share this two- to six-syllable, rapidly paced structure. Foraging and pair-contact calls of most are similar as well. All recordings except A by Whitney.

single syllables (e.g., Fig. 7E [left side]) that sound much like the calls of *Acrobatornis.* Scold or mobbing vocalizations of *Cranioleuca* (we know most species) consist of 2–6 emphatic, sharp syllables (vertical orientation in spectrograms) delivered in rapid succession (e.g., Fig. 7D and E [two examples on right side]). In *Cranioleuca,* pairs rarely duet, although both members may sing simultaneously in an unsynchronized manner. As we observed for *Acrobatornis,* duets are most frequently heard in response to tape playback.

Asthenes.—To place our discussion of relationships of *Asthenes* to *Acrobatornis* in perspective, it is necessary to express our view that *Asthenes* includes two, possibly three, distinct lineages, the evolutionary histories of which have probably been independent since pre-Andean times. It serves to separate the two most obvious ones, generally, by habitat and nest architecture. The "stick-nesting" group inhabits woody brush and rocks and is not dependent on grassland (e.g., Chaco woodland and scrub;

arid and semi-arid interandean valleys; barren altiplanos; one in Brazilian serra), and builds sturdy nests of sticks (depending on their availability) lined mostly with wool and grass. The second, "grass-nesting," group is completely dependent on grassland (with or without scattered shrubs and rocks; e.g. grassy páramos; *Festuca*-dominated hillsides and valleys; one in grassy coastal marshes from extreme southern Rio Grande do Sul to Buenos Aires, Argentina) and builds nests of grasses and other herbaceous material; most species use no or few sticks (far-southern *A. anthoides* [Austral Canastero] may be an exception). A thorough definition of this division, which finds parallel in distinct morphotypes, vocalizations, and ecologies, is beyond the scope of this paper. Species limits within *Asthenes* have been the subject of much debate over the years and, unfortunately, recent modifications that seem to have gained general acceptance (e.g., the *A. dorbignyi* [Creamy-breasted Canastero] complex) have been extraordinarily poorly documented. For comparison with *Acrobatornis,* we selected some typical members of our "stick-nesting" group of *Asthenes* (see "Specimens Examined," above, Table 1, and Fig. 9).

Bill lengths and overall shapes vary considerably within stick-nesting *Asthenes,* but small-billed species like *A. baeri* (Short-billed Canastero; Fig. 2D, Table 1) and *A. patagonica* (Patagonian Canastero) closely approach *Acrobatornis.* These are also the lightest members of the group, with body mass essentially like *Acrobatornis* (data for *baeri* in Table 1). Like *Cranioleuca, Asthenes* have tail/wing ratios greater than 1. Stick-nesting *Asthenes* have blunt-tipped or weakly acuminate rectrices that are not excised. They forage on the ground or low in brush and rocks with short gleans, reaches, and probes, often moving quickly between places of concealment, seldom ascending to heights of more than about 1 m except to sing or for nesting.

Two types of songs or song-like vocalizations are shared by stick-nesting *Asthenes,* each of generally uniform pattern and cadence (but a few differ appreciably in auditory quality) across the group. One begins with well-separated syllables then rapidly accelerates through several (at least 5) seconds, often descending slightly through the terminal third. Examples are shown in Fig. 8A and C (selected from recordings of all species of *Asthenes*). Figure 8E shows a variant of this song-type in which pace is much slower through about the first two-thirds, and syllables are finely modulated (and sound harsher), probably communicating a different message. In all respects, including auditory quality (which is especially difficult to judge from a spectrogram), this song-type of *Athenes* is remarkably similar to the song of *Acrobatornis* (compare with Fig. 6A, B, C). The second song-type is a rattling series of rapidly paced syllables that begins quietly, quickly crescendos, and then trails off as it slows

down (Fig. 8B, D, F). We have not heard a song of this type from *Acrobatornis*. Among all stick-nesting *Asthenes*, the songs of *A. baeri* (of semiarid brush and woodland from extreme southern Brazil to central Argentina) and *A. dorbignyi* (of arid and semiarid, brushy valleys and slopes of the Andes of southern Peru to central Argentina) are most similar to songs of *Acrobatornis*; indeed *A. dorbignyi* and *A. baeri* appear to be sister species elevationally allopatric in the north and perhaps parapatric farther south, in Mendoza, Argentina. Like *Acrobatornis*, calls of *Asthenes* species (Fig. 8A, E, G) are sharp, single syllables similar to the introductory syllables of the song. Some canasteros occasionally sing duets, especially at territorial encounters or in response to tape-recording playback; an example is shown in Fig. 8H (*A. patagonica*).

Thripophaga.—The bill of *T. fusciceps* (Plain Softtail; Fig. 2F, Table 1) is proportioned much like that of *Acrobatornis*, but is larger; body mass is correspondingly greater as well. The rectrices of the four species currently included in *Thripophaga* are wide, soft, and blunt-tipped (the poorly known *T. berlepschi* [Russet-mantled Softtail], which probably does not belong in this genus, somewhat more pointed). We have field experience only with *T. macroura* (Striated Softtail) and *T. fusciceps* (Plain Softtail). Both forage with mixed-species flocks, mostly in the middle strata of dense, vine-rich, humid, lowland forest, by hitching and crawling upwards and laterally through tangles with the tail partially spread, reaching and gleaning (rarely hanging) from bark, vines, and especially dead foliage trapped in such places. They are not scansorial. Songs and calls of *T. macroura* and *T. fusciceps* are very similar in structure and auditory quality. A long song of *T. macroura*, selected to show maximum similarity to *Acrobatornis*, is shown in Fig. 7D; most songs are introduced by a single or two well-separated, loud syllables followed immediately by a short burst of tightly spaced syllables, the whole lasting less than about 1.5 sec. Although cadence and pace of the long song resemble the song of *Acrobatornis*, structure of individual syllables, and thus auditory quality, are quite different.

Phacellodomus.—The smallest member of *Phacellodomus*, *P. sibilatrix* (Little Thornbird), is slightly larger than *Acrobatornis* (Table 1, tail/wing ratio 1.1). Like other members of the genus, its bill is also differently shaped, with a hump above the nares and steeply sloping culmen (Fig. 2G). Rectrices of *Phacellodomus* thornbirds are blunt-tipped. They forage primarily with reaches and gleans on the ground and in low brush and thickety growth, often hopping on the ground. Across the genus (we do not know *P. dorsalis* [Chestnut-backed Thornbird], of the middle Marañon valley of n. Peru), male thornbird songs are delivered from prominent perches (bush- or treetops, for instance, always near the nest) and con-

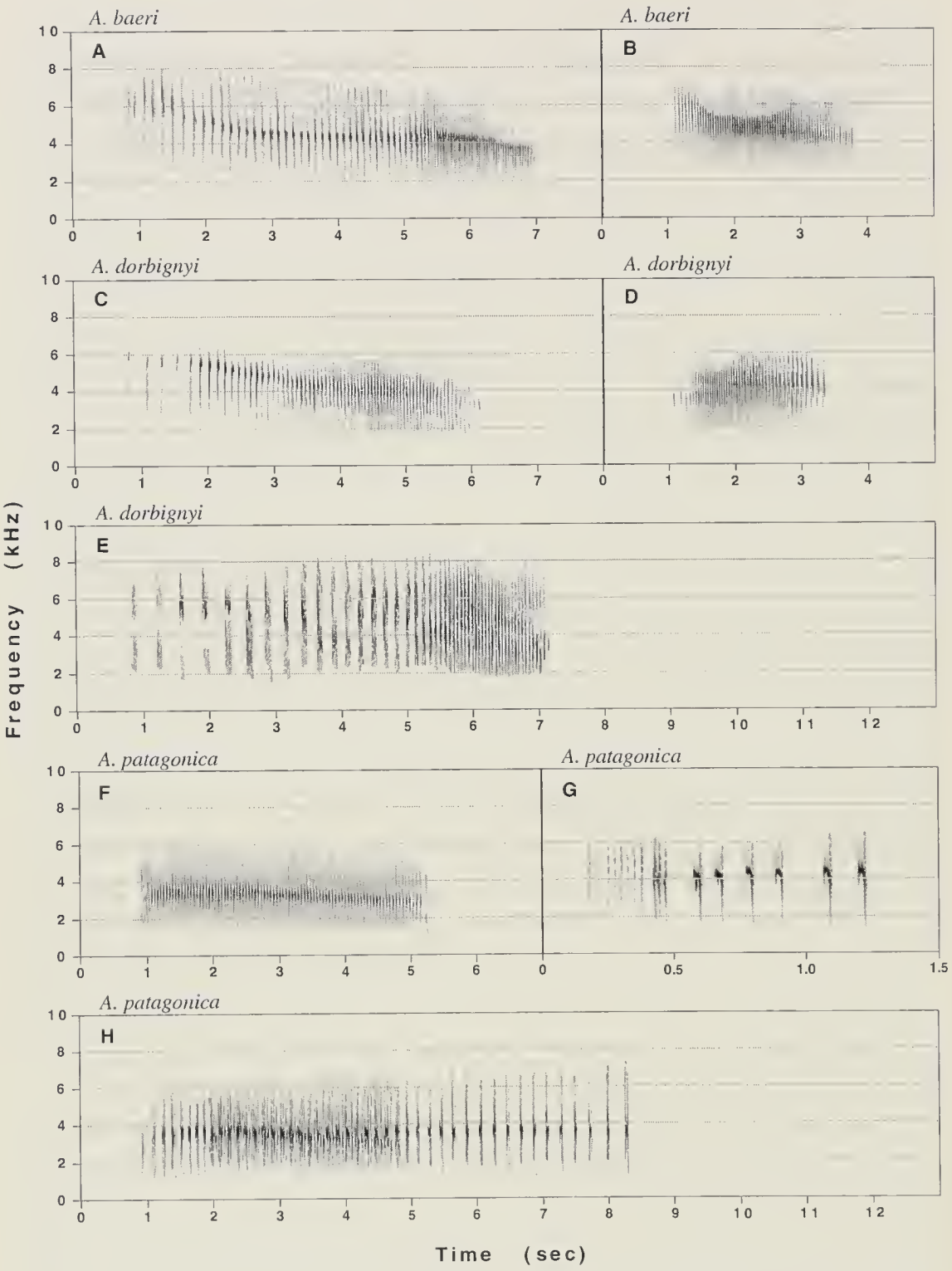

FIG. 8. Sound spectrograms of vocalizations of selected stick-nesting *Asthenes* species. A. *A. baeri,* song after conspecific tape playback (same as natural). Introductory syllables are like one common type of pair-contact call. Argentina: Salta, 05 km S. Rivadavia, 27 Oct. 1989, 260 m. LNS 46142. B. *A. baeri,* a second song-type. Argentina: Salta, 50 km N. J. V. Gonzalez, 28 Oct. 1989, 390 m. LNS 46166. C. *A. dorbignyi,* natural song. Argentina: Jujuy, 13 km N. Humahuaca, 4 Jan. 1988, 3300 m. LNS 43944. D. *A. dorbignyi;* a

sistently comprise series of evenly spaced syllables on a steady or slightly ascending and descending frequency, the whole lasting about 2–4 sec and repeated at intervals of several seconds. Examples are shown in Fig. 9 (A, C, D; selected from recordings of all species except *dorsalis*). Females and immatures sing and sometimes duet with males (Fig. 9A). Individuals are capable of singing several variants of the song; some (especially those in duets) are considerably longer and more complex than the "normal" songs shown in the figures. Calls of *Phacellodomus* delivered while foraging are sharp, penetrating syllables (e.g., Fig. 9B). Somewhat different, single-syllable calls are given while scolding or mobbing. Although songs of *Phacellodomus* are not similar to those of *Acrobatornis* in overall pattern, some variants (e.g., female part of duet in Fig. 9A) sound like the beginning of songs of *Acrobatornis*.

Xenerpestes.—The two species of *Xenerpestes* are little-known, and their relationship within the Furnariidae (in fact, whether they are furnariids at all), is poorly corroborated. One anatomical specimen exists (National Museum of Natural History), but has not been analyzed. Mensural data for *X. singularis* presented in Table 1 (see Fig. 2H for bill and tarsus shapes) are remarkably similar to those of *Acrobatornis*, although *Acrobatornis* is about 15% heavier and has a thicker, more powerfully clawed tarsus. The average tail/wing ratio of four *Xenerpestes singularis* is 0.88, essentially identical to *Acrobatornis* (0.89). Within Furnariidae, the black-and-gray definitive plumage of *Acrobatornis* is approached, albeit superficially, only by the two members of *Xenerpestes*, both of which have restricted distributions in nw South America: *X. minlosi* (Double-banded Graytail) and *X. singularis* (Equatorial Graytail). Both are basically grayish above and have pale superciliaries; *X. minlosi* is black-capped, like *Acrobatornis*; *X. singularis* lacks a contrasting cap and has a rufous-streaked forecrown. *Xenerpestes minlosi* is mostly whitish below, and has two fairly conspicuous, white wingbars; *singularis* has yellowish,

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second song-type. Argentina: Jujuy, 30 km W. La Quiaca, 05 Jan. 1988, 3640 m. LNS 43952. E. *A. dorbignyi*, "harsh" version of natural song-type shown in C (this example also natural). Same individual (and part of same recording) as in D. LNS 43952. F. *A. patagonica*, natural song. Argentina: Rio Negro, 8 km E. Villa Regina, 7 Jan. 1988, 485 m. G. *A. patagonica*, calls of a single individual. Argentina: Chubut, 08 km NNW Trelew, 12 Jan. 1988. LNS 46108. Context for these calls unknown; possibly pair-contact calls. H. *A. patagonica*, pair duet involving same individual shown in F, after playback of song shown in F. LNS 43960. Note almost identical songs, both types, of *A. baeri* and *dorbignyi*; also similarity of the three *Asthenes* species shown in B, D, and H, and of these to song of *Xenerpestes minlosi* in Fig. 9E. Note close similarity of songs of *A. baeri* and *dorbignyi* A and C to songs of *Acrobatornis* in Fig. 6B and C. All recordings by Whitney.

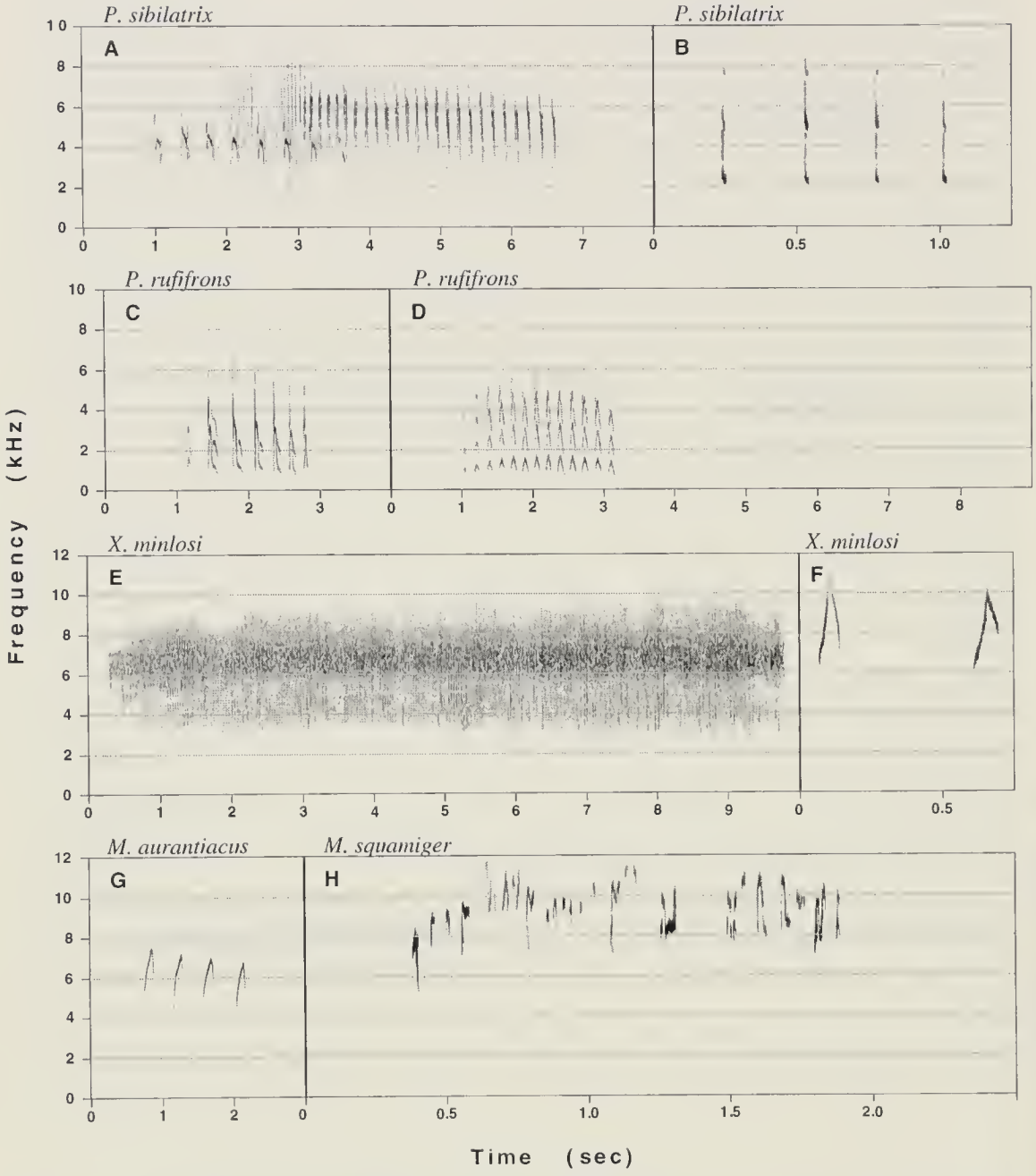

FIG. 9. Sound spectrograms of vocalizations of some other stick-nesting furnariids, and the highly scansorial *Margarornis squamiger.* A. *Phacellodomus sibilatrix,* natural duet at nest. Presumed male begins with more widely spaced syllables centered at about 4 kHz, joined by presumed female singing rapid series at higher frequency. Argentina: Salta, 50 km N. J. V. Gonzalez, 28 Oct. 1989, 390 m. LNS 46163. One common type of male song is similar to that shown in this duet. The presumed female song shown here is similar to the beginning of the song of *Acrobatornis* (Fig. 6B and C). B. *P. sibilatrix,* natural calls, apparently pair-contact. Argentina: Salta, 75 km E. J. V. Gonzalez, 30 Dec. 1987, 330 m. LNS 43831. C. *P. rufifrons,* natural song. Song-type repeated at fairly regular intervals from a stationary perch, often in active nest tree. Brazil: Mato Grosso do Sul, NW, Miranda at "Pousada Caiman," 19 July 1995. D. *P. rufifrons,* natural song. Different song-type from that shown in C. We believe individuals give both song types, and some others; thornbirds

black-streaked underparts and plain, grayish wings. Rectrices of both *Xenerpestes* are grayish and blunt-tipped. They forage actively in the subcanopy of humid forest, almost always with mixed-species flocks, hopping and hitching along the uppersides of limbs, occasionally hanging on leaf-clusters, rarely inverted from limbs, performing gleans and short reaches. They are not scansorial, but Ridgely and Tudor (1994:129) noted for *X. singularis* that "occasionally one briefly creeps along a branch." *Xenerpestes minlosi* often forages in dead leaves and leaf-clusters, and often hangs briefly from foliage. Similar behaviors of *X. singularis* were described by Parker and Parker (1980). The voice of *X. minlosi* is a long, extraordinarily rapidly paced, chattering series of syllables on a steady frequency, beginning quietly and quickly attaining an increased amplitude with slight pulses at irregular intervals; the whole lasts from 3–12 sec (Fig. 9E). We believe pairs sometimes duet. Calls are sharp, thin, almost bisyllabic notes (Fig. 9F). The song differs from that of *Acrobatornis* in its rapid beginning and overall rapid pace, but is approached by the tightly spaced ending of long songs of *Acrobatornis.* One individual singing in the *Acrobatornis* duet shown in Fig. 6D sounded much like *Xenerpestes minlosi* shown in Fig. 9E. In our opinion, the song of *Xenerpestes minlosi,* together with other evidence gathered to date, clearly places this genus in the Furnariidae.

Metopothrix.—Metopothrix aurantiacus (Orange-fronted Plushcrown; sole member of the genus), like *Xenerpestes,* is a small, phylogenetically obscure furnariid bearing marked structural resemblance to *Acrobatornis* (Fig. 2I, Table 1). Its tarsus and foot appear to be somewhat stronger than those of *Xenerpestes,* thus closer to *Acrobatornis,* and the average tail/wing ratio of three specimens exactly matches *Acrobatornis* (0.89). Rectrices of *Metopothrix* are grayish and blunt-tipped or slightly pointed. *Metopothrix* usually forages with mixed-species flocks in the subcanopy

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have complex vocal repertoires. Brazil: Bahia, 06 km NW Boa Nova, 9 Mar. 1996. E. *Xenerpestes minlosi,* song after playback (same as natural but longer). Dark band at about 7 kHz is insect noise. Panama: Darién, Cana airstrip in Parque Nacional Darién. Note similarity with songs of stick-nesting *Asthenes* species in Fig. 8B, D, and F, and with songs of *Acrobatornis* in Fig. 6B and C, especially the rapidly paced ending of those songs. It also seems quite similar to one of the individuals singing in the duet of *Acrobatornis* in Fig. 6D. F. *X. minlosi,* natural pair-contact calls. Same individual as E. G. *Metopothrix aurantiacus,* natural song. Peru: Madre de Dios, near Atalaya above "Hacienda Amazonia" lodge, 8 July 1989, about 600 m. Songs vary from 2 to 5 syllables (3 most common). H. *Margarornis squamiger,* natural calls of foraging birds, context unknown. Songs of all *Margarornis* species are sharp, high-frequency syllables like these, but are delivered in a rapid, steady series lasting about 1 sec. All recordings by Whitney.

of forest and well-developed second-growth, mostly in river-created habitats (medium/old whitewater islands, river edge, and foothill forest near river floodplains) in upper Amazonia. It performs gleans and reaches in live foliage and vine tangles, often at or near the periphery of trees, paying particular attention to the undersides of leaves, including large leaves like those of *Cecropia* species, and very small leaves like those of Leguminosae. Individuals may hang inverted for several seconds at a time, and sometimes crawl in an inverted position. The song of *Metopothrix* is an inconspicuous series of 3–5 evenly spaced, high, thin syllables lasting 1.5–2.5 sec (Fig. 9G). The birds nearly always travel in pairs or family groups, and we have heard a variety of other, quiet, intrafamilial vocalizations. The song and these other vocalizations show little resemblance to those of *Acrobatornis.*

Margarornis.—The three or four (including *M. bellulus* [Beautiful Treerunner]) currently recognized species of *Margarornis* treerunners are small furnariids (Rudge and Raikow 1992a) that inhabit humid montane forest of southern Middle America and the Andes. The bill of *Margarornis squamiger* is shaped much like that of *Acrobatornis,* but is slightly longer, as is the tail/wing ratio (average of 3 specimens 0.95); body mass is also greater (Fig. 2J; Table 1). Rectrices are acuminate with the rachis extending slightly beyond the feather vanes. *Margarornis* species forage with mixed-species flocks in the forest interior. They are highly scansorial, almost constantly creeping along limbs, both upper- and undersides, and sometimes up tree trunks, performing gleans and probes in moss, epiphytic growth, and dead leaf clusters. They sometimes use the tail as a prop when stationary (Slud 1964, Wetmore 1972, pers. observ., all species). Individuals may hang inverted on balls of moss or leaf clusters for several seconds. The scansorial behavior of *Margarornis* species appears to be much like that of *Acrobatornis,* although we have not been able to determine whether the locomotory and grasping action of the legs and feet of the two are the same. Dissection of hindlimb musculature of *Acrobatornis,* in comparison with that reported by Rudge and Raikow (1992b) for their *Margarornis* assemblage, would perhaps be enlightening in this regard. *Acrobatornis* spends much time hanging from and crawling through foliage, a search-method rarely practiced by *Magarornis* species. Songs of all *Margarornis* treerunners consist of short, sharp, high-frequency syllables delivered in a steady series lasting about 1 sec. Calls are like individual syllables of the song, but are delivered at irregular intervals (i.e., not in repetitive series; Fig. 9H, selected from recordings of all species). Their vocalization seem quite different from those of *Acrobatornis.*

So what is Acrobatornis most like?—Overall morphological compari-

sons from both Table 1 and Fig. 2 show particularly close parallels in bill shape, tail/wing ratio, and all standard absolute measurements between *Acrobatornis, Metopothrix,* and *Xenerpestes,* and lesser similarity of these with *Margarornis.* The acuminate and strongly excised central rectrices of *Acrobatornis* are different from the blunt rectrices of these others, but are like several species of *Cranioleuca.* Among stick-nesting *Asthenes, A. baeri* and *A. patagonica* seem close to *Acrobatornis.* We judge plumage parallels (overall pattern and regions of contrast) strongest with *Cranioleuca* (notwithstanding that no species are colored like *Acrobatornis*) and *Xenerpestes.* Comparisons of vocalizations, especially songs and adult contact (foraging) calls, show a strikingly close similarity to one song-type of some stick-nesting *Asthenes,* and notable parallels with *Xenerpestes.* Single-syllable foraging or pair-contact calls of *Acrobatornis* appear most like those of montane *Cranioleuca* species, but this is more complicated by the difficulty of judging homology of these vocalizations. The hanging and inverted-scansorial foraging maneuvers of *Acrobatornis* are approached most notably by *Margarornis* and *Cranioleuca* and, to a lesser extent, *Metopothrix* and *Xenerpestes,* and some other arboreal furnariids. *Asthenes* are highly terrestrial foragers, and bear no resemblance to *Acrobatornis* in this regard.

Our intrafamilial comparisons of morphology, vocalizations, and foraging behavior, together with nest architecture and placement discussed by Whitney et al. (1996), suggest that *Acrobatornis* is related to stick-nesting *Asthenes* canasteros and *Cranioleuca* spinetails, and may be the closest relative of the *Xenerpestes* graytails and the monotypic *Metopothrix.* It is, of course, impossible at the moment to know how many of the similarities among these genera might be the result of convergence. Our hypotheses are, at least, supported by multiple, corroborative parallels, and may be helpful in orienting future, especially biochemical, investigation. Pertinent specimens are at hand.

On the origin of Acrobatornis.—As pointed out by Remsen (1984), "Although reconstructions of historical zoogeographic events often contain more speculation than warranted by available data, such historical hypotheses are a necessary part of a zoogeographic and taxonomic analysis." We postulate that *Acrobatornis fonsecai* represents a relict from an expansion of stick-nesting furnariids from a (probably arid or semi-arid) Chaco-Patagonian/Pantanal distributional center that survived in arboreal habitats on ancient and stable soils in southeastern Bahia. Soils in the restricted region from Feira de Santana south to the vicinity of Camacan and Pau-Brasil are formed primarily of decomposed crystalline rock of lower Precambrian age known as the Jequié Complex, and are among the oldest soils on the planet (Caldeira 1954, RADAMBRASIL 1981). The

entire known distribution of *Acrobatornis* is encompassed in this area. *Acrobatornis* appears to be absent from forests on the sandy fluvio-marine plain ("Planicie fluviomarinha" RADAMBRASIL 1981). It may inhabit evergreen seasonal forest ("mata de tabuleiro"), however, where the cocoa-growing region approaches the coast between Itabuna and Ilheus. This forest is also mostly on soils of the Jequié Complex. The fact that these soils are extremely old and have apparently been stable for a long period of time may help explain the peculiar, relictual distribution of *Acrobatornis.*

As the arid and semi-arid periods that had originally allowed it to reach the region eventually gave way to a more mesic environment with taller trees, *Acrobatornis* survived by gradually adapting to build its nests in the relatively xeric crowns of trees, especially Leguminosae. These wide, leguminaceous canopies, with their small leaves and open, layered stratification of limbs, are indeed hot and dry, supporting virtually no epiphytic growth. *Acrobatornis* may have managed to survive through successful ecological adaptation; we suspect the nest and vocalizations have undergone little structural modification.

A quite different hypothesis of origin of *Acrobatornis* in the humid forest of southeastern Bahia gives primary importance to analysis of distributions of birds syntopic with it today. Almost all (if not all) birds inhabiting the lowland forest of southeastern Bahia, from terrestrial species to canopy species, are unequivocally most closely related to (and probably derived from) Amazonian stock (Willis 1992, Whitney et al. 1995). Why should *Acrobatornis* be any different? For *Acrobatornis,* unlike all other birds in this region of Bahia, it is difficult to identify and justify a contemporary link to an Amazonian relative. In this context, however, we recall various similarities to upper Amazonian *Metopothrix* and, in the subtropical forests of the east slope of the Andes and in trans-Andean lowlands, *Xenerpestes.* Could there be (or could there have been) an *Acrobatornis*-like bird in the vast and little-known canopies of Amazonia? The answer to this riddle may lie in elucidation of such poorly understood factors as edaphic habitat maintenance and variable distribution of vegetation types.

Conservation: the destiny of Acrobatornis.—The area of occurrence of *Acrobatornis fonsecai* lies entirely within the nucleus of the cocoa-growing region of southern Bahia. Up to now, it has maintained apparently viable numbers in harmony with intense anthropogenic alteration of its habitat and pervasive human presence (Fig. 10). Although virtually no undisturbed forest remains in the lowlands of the Rio Jequitinhonha-Rio de Contas interfluvium, it is clear that the persistence of the "cabruca" canopies shading the cocoa guarantees the survival of a considerable por-

FIG. 10. House and cocoa plantation on the side of the major highway BR-101, about 14 km N. of Itabuna, Bahia. Tall, native trees shading cocoa plantations such as this provide acceptable breeding habitat for *Acrobatornis fonsecai* and a wide variety of other birds. A nest of *Acrobatornis* is visible as a dark spot in the upper left of the tall tree in the center of the photograph. Photo by Whitney.

tion of the indigenous canopy fauna and flora, including the avifauna (Alves 1990, pers. observ.), and maintains corridors for fauna only seasonally or temporally dependent. The cabruca system of growing cocoa has preserved, to a considerable extent, the humid microclimate upon which many forms of life depend, and must be responsible on a large scale for maintenance of the local hydrologic regime. Cabruca canopies are in some areas almost continuous over large tracts, and hold magnificent adult trees of a wide variety of species. Many individuals of these mature trees must be near the end of their lifespans, however, and there are no seedlings to regenerate them because of constant weeding of the understory in cocoa plantations. Consequences of this were summarized by Mori et al. (1981): "A system of clear-cut and burn with the subsequent replacement of native trees by monotypic stands of [introduced] *Erythrina fusca* has been developed. In this system, banana trees are used to shade the young cocoa plants and to provide income until the cocoa trees produce fruit. Fertilizers, herbicides, and pesticides are used in both systems [this and cabruca] but more so in the cut-and-burn system." This system is called "derruba total" (Alger and Caldas 1996).

Cocoa was introduced into southern Bahia from the Amazon in 1746, and has been the most important crop in that region ever since (Mori et al. 1983). In their concise and well-balanced discussion of the history of cocoa cultivation and the current socioeconomic problems confronting the cocoa growers of southeastern Bahia, Alger and Caldas (1996) reported that during a brief period in the 1970s, cocoa from southern Bahia was the second most important export for Brazil, after coffee. During this era, more than half a million hectares were planted in cocoa, and the industry flourished. Between 1986 and 1992, however, the international price for cocoa fell from US $2500 to $1000 per ton, hitting the industry hard. Then, in 1989, came the accidental introduction of the fungus *Crinipellis perniciosa,* which causes the disease known as "witch's-broom." According to the Executive Commission for the Economic Recovery of the Cocoa Industry (CEPLAC), as of March 1995, the disease had spread through more than 70% of the cultivated region. Control of the fungus was expensive and ultimately not effective. Cocoa production plummeted, with dire consequences for the livelihoods of tens of thousands of people and, concomitantly, for the remnant forests of southeastern Bahia. For example, the newspaper *A Tarde* of Salvador, Bahia, for 16 Feb. 1996 (article by Rosa M. Carvalho), reported that Hershey, the largest chocolate producer in the United States and perhaps the biggest buyer of Bahian cocoa, was on the verge of terminating contracts with Bahian growers because of the drastic decline in cocoa production. And Alger and Caldas (1996) reported how plantation owners, although often with reluctance, have little choice but to cut their valuable old trees and sell the timber for immediate cash. They explained, "The shift from cocoa to other crops or for livestock pasture is not considered remunerative. Deforestation for timber sale is generating pasture more because of lack of alternatives than enthusiasm for livestock raising." They went on to describe how many of the largest plantation owners, faced with steady losses, are highly amenable to preserving their remnant forests, but receive little support from the government to do so, and emphasized the importance of establishing economic incentives for land preservation, such as subsidies for formation of private reserves.

As it stands now, there is not one officially protected area of forest in the range of *Acrobatornis,* although it may eventually be found in the nearby Una Reserve, the avifauna of which is poorly known. This reserve is the stronghold of one of the rarest primates in the world, *Leontopithecus chrysomelas* (Golden-headed Lion Tamarin), which has a distribution almost exactly coincident with that of *Acrobatornis:* remnant lowland forest between the Rio de Contas and the Rio Jequitinhonha. Even a tribe of Indians, the Kamakan, was indigenous to the still more restricted region

between the Rio de Contas and the Rio Pardo; the modern town, Camacan, takes their name. The last member of the Kamakan died in 1938 (Viveiros de Castro 1986).

The only practical means that we can imagine of preserving a population of *Acrobatornis* and the other fauna in this region is the immediate purchase of two large, separate blocks, one in the serra das Lontras and one in the serra Bonita, that encompass forest from the highest elevations in these ranges down to near sea-level. Such blocks must incorporate extensive cabruca canopies in contact with healthy forest canopies. The cocoa could then be removed and seedlings of native tree species planted to replace the aging adults. Local people, especially large land-owners, must be integrally involved in establishment and maintenance of these forest reserves. This land is for sale today, and the price and socio-political climate are favorable (Alger and Caldas 1996).

We will never cease to be amazed at how this striking little bird that constructs conspicuous stick-nests in treetops along the congested highway BR-101 could have been overlooked so completely. Its discovery serves to remind us of how much remains to be learned, even as it fades from existence.

ACKNOWLEDGMENTS

This description benefitted from the generous collaboration of Phyllis Isler (who produced the sound spectrograms from our recordings), P.S.M. da Fonseca (whose assistance and enthusiasm in the field were unflagging), Dan Lane (who illustrated the skulls and tarsi), Claudia Bauer (who helped in the field and in making the map), Robert Barth (who assisted in and funded part of the October 1995 field work); and Morton Isler (who produced the morphological table from our data): their contributions are tremendously appreciated. We are grateful to J. V. Remsen, Jr. and Steven Cardiff of LSUMZ, and Robert Ridgely, David Agro, and Sally Conyne of ANSP for allowing us to examine specimens in their care. Steven Cardiff and Donna Dittmann also oversaw preparation of the skeleton of the new genus, and Steve prepared the study skin that documents its identity. Hannah Gould of the Univ. of Texas at Austin helped us locate pertinent references, and Johann Becker of the National Museum of Rio de Janeiro gave us valuable advice on questions of nomenclature. Francisco Mallet-Rodrigues and Inge M. Schloemp helped us in a variety of ways. Howard Wilson assisted in making black-and-white images from Hi-8 format video tape. Gary Graves and J. V. Remsen, Jr. gave us helpful criticism of the manuscript, and Charles Blem assisted in seeing that it was published promptly. Mark and Allison Duffel of "Mr. Wizard's" in Austin, Texas have been especially helpful in keeping our recording equipment in optimal condition, often on short notice, and Holland Photo of Austin produced the black-and-white photos in the figures. Field Guides Incorporated, of Austin, Texas, generously financed part of our expenses for research in southern Bahia, and tour participants Jane Brooks, James Plyler, Thomas Raque, John and Barbara Ribble, and Polly Rothstein helped Whitney make important observations in March 1996. Finally, we are grateful to Paul Donahue for his attractive frontispicce painting of the new genus and species.

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WILSON ORNITHOLOGICAL SOCIETY MEETING

The 78th Meeting of the Wilson Ornithological Society will be held 17–20 Apr., 1997, Kansas State Univ., Manhattan, KS. The Society will meet jointly with the Kansas Ornithological Society. Registration materials and call for papers will be sent to members in December 1996. Inquiries about the scientific program should be directed to John C. Kricher, Biology Dept., Wheaton College, Norton, MA 02766 (508-286-3950; jkricher@wheatonma.edu). Local chair is John L. Zimmerman, Div. Biology–Ackert Hall, KSU, Manhattan, KS 66506-4901 (913-532-6659 or -6615).

Wilson Bull., 108(3), 1996, pp. 434–448

THE NEST AND NESTING ECOLOGY OF *ACROBATORNIS FONSECAI* (FURNARIIDAE), WITH IMPLICATIONS FOR INTRAFAMILIAL RELATIONSHIPS

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ABSTRACT.—Descriptions of the nest and nesting ecology of *Acrobatornis fonsecai* (Pink-legged Graveteiro), a newly described genus and species in the Furnariidae, are presented. Nests, constructed of twigs and sticks, are single-chambered, well-lined with mosses and leaves (one examined in detail), and situated in the canopy of tall trees. In October 1995, we located 131 nests in 72 trees at 54 sites. The average number of nests/tree was 1.8 with a maximum of five nests in a single tree; apparently only one nest/tree is active. "Extra" nests were often smaller than active nests, and at least sometimes had no entrance or chamber. We postulate that these nest-like structures represent dummy or cock nests to confuse predators or parasites (it certainly worked on us), and may serve as resource stores (i.e., construction materials and nest foundations). Brief observations indicated that immatures (probably offspring) help adults in nest construction, and may help feed food-begging juveniles. Comparison with other, possibly related, furnariids, suggests that nest architecture of *A. fonsecai* is most similar to that of the "stick-nesting" group of *Asthenes* canasteros, for which nests are relatively well known, but is also similar to some *Cranioleuca* spinetails and perhaps to the *Xenerpestes* graytails and the *Metopothrix* plushcrown, which are poorly known. Our data supplement the discussion of morphological, vocal, and behavioral comparisons of the same groups presented by Pacheco et al. (1996). We postulate that stick-nesting in Furnariidae arose in a pre-Andean, Chaco-Patagonian/Pantanal center, and provide some theories on the evolution of this behavior. *Received 23 April 1996, accepted 21 May 1996.*

RESUMO.—Descrição do ninho e dados ecológicos da nidificação de *Acrobatornis fonsecai* (Acrobata), um novo gênero e espécie de Furnariidae recentemente descrito são apresentados. Os ninhos, construídos de gravetos, possuem uma única câmara bem forrada com musgos e folhas (N = 1 examinado em detalhe), e são situados na copa de árvores altas. Em outubro de 1995 foram localizados 131 ninhos em 72 árvores em 54 pontos diferentes. O número médio de ninhos por árvore foi de 1,8, com um máximo de cinco ninhos em uma única árvore; aparentemente apenas um ninho por árvore é ativo. Os ninhos "extras" são geralmente menores do que os ninhos ativos e, ao menos às vezes, não apresentam entrada ou câmara. É postulado que estas estruturas representem "ninhos falsos" para confundir predadores ou parasitas (como aconteceu com os autores) ou, talvez, para servir como reserva de recursos (i.e., material de construção e "alicerce" de ninhos). Breves observações indicam que imaturos (provavelmente filhotes de uma ninhada anterior) ajudam adultos na construção do ninho e, talvez, colaborem na alimentação de jovens. Comparações com outros, possivelmente aparentados, furnarídeos, sugere que a arquitetura do ninho de *A.*

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fonsecai tenha mais semelhança com aqueles do grupo de *Asthenes* "construtores de ninhos de graveto," para o qual os ninhos são relativamente bem conhecidos, mas também apresenta similaridades com aqueles de algumas *Cranioleuca* e talvez com aqueles de *Xenerpestes* e *Metopothrix*, os quais são insuficientemente conhecidos. Os dados sobre o ninho e nidificação complementam a discussao de morfologia, vocalização e comportamento em comparação aos mesmos grupos conforme apresentados por Pacheco et al. (1996). É teorizado que a contrução de ninhos de gravetos em Furnariidae surgiu num período pré-andino no centro Chaco-Patagônia-pantanal, e são fornecidas algumas teorias sobre a evolução deste comportamento.

Nest architecture and placement have been considered important in judging systematic relationships in the Neotropical family Furnariidae (Vaurie 1971, 1980), and we concur that data on nests, at least insofar as definition of basic nest-type, are desirable in any analysis of intrafamilial relationships of this complex assemblage of birds. We are also in full agreement with Narosky et al. (1983) that caution regarding assumptions of relatedness based on current classifications or on nesting similarities must be maintained. Data on nests should be overlaid with as many other potentially informative data as possible. This report on the nest and nesting ecology of the recently discovered and described *Acrobatornis fonsecai* (Pink-legged Graveteiro; Pacheco, et al. 1996), a new genus and species in the Furnariidae, supplements the discussion of its relationships based on intrafamilial comparisons of morphology, vocalizations, and behavior presented by Pacheco et al. (1996). Distribution of *A. fonsecai* in the remnant lowland forest of southeastern Bahia, Brazil, was mapped by Pacheco et al. (1996; Fig. 4).

Description of the nest of Acrobatornis fonsecai.—As seen from the ground, the nest of *Acrobatornis fonsecai* is a globular, ovoid, or roughly rectangular structure of twigs and sticks, usually situated in a fork of branches, sometimes on top of a limb if angled less than about 30° above the horizontal, and inside the crown of a tall tree surrounded by or adjacent to other tall trees (Fig. 1). Because nests are generally conspicuous in treetops, sometimes in leafless trees, we located them easily with visual searches, mostly from roadsides. These nests may have been overlooked or ignored by the many observers who have traversed this region in the past because of their superficial similarity to nests of *Phacellodomus rufifrons* (Rufous-fronted Thornbird) which, however, typically builds much longer nests that hang in a vertical column from the periphery of isolated trees (Skutch 1969a, Thomas 1983). Like those of *A. fonsecai*, nests of thornbirds are also variable in shape and size, with some, probably unfinished, nests being constructed around upright branches or even thin tree trunks (Figs. 2, 3). Such nests are often smaller than normal, and similar in outward appearance to those of *A. fonsecai*.

FIG. 1. Nest tree of *Acrobatornis fonsecai* at the edge of a mixed cocoa and banana plantation along a road near Arataca, Bahia. Most nest trees were in closer proximity to other tall trees. This *Senna multijuga* tree held five nests (see Fig. 2). Photos in this and other figures by Whitney.

Between 4 and 12 October 1995 we plotted a total of 131 nests of *Acrobatornis fonsecai* in 72 nest trees at 53 different sites in the Itabuna-Camacan region of southeastern Bahia (see Fig. 4 in Pacheco et al. [1996]). At 36 sites we observed only a single nest tree, at 16 sites, two nest trees, and 1 site had four trees with nests. At sites with more than one nest tree, we noted that these were generally less than about 100 m apart (unless on opposite sides of a road), but that they were rarely immediately adjacent. We do not know whether these separate trees were occupied by separate pairs of *A. fonsecai.* As can be deduced from the numbers above, individual trees usually held more than one nest. Of the

FIG. 2. Nest tree (*Senna multijuga*; see Fig. 1) of *Acrobatornis fonsecai* near Arataca, Bahia. Five nests are visible; we do not know if any were active in October 1995.

total of 72 nest trees we found in October, 31 (43%) held one nest, 27 (37%) held two nests, 11 (15%) held three nests, 2 held four nests, and 1 tree had five nests (Figs. 1, 2). The average number of nests/tree was 1.8. Nest-height varied considerably with tree height, but nests were always in the upper ⅓, usually in the upper ¼, of trees. Most nests were in excess of about 20 m above ground, and we estimated some as higher than 30 m.

Acrobatornis fonsecai builds nests mostly in mature trees of the family Leguminosae. Of the 72 nest trees located, 37 (51%) were members of the genera of Leguminosae mentioned in the "habitat" section of Pacheco et al. (1996; except that no nests were found in *Inga* species), 25 (35%) were not identified to family (but we suspect that many of these were male *Erythrina* species), and 10 were leafless trees (most of which we suspect were Leguminosae that had dropped their leaves). Leguminosae are among the dominant trees along roadsides over cocoa plantations in the range of *A. fonsecai*. This notwithstanding, we do not estimate that Leguminosae were so overwhelmingly more numerous than other tall trees that this could account for the fact that *A. fonsecai* nested mostly in Leguminosae. A more plausible explanation might be that the relatively open nature of the crowns of Leguminosae, and the fact that many had

FIG. 3. Nest tree of *Phacellodomus r. rufifrons* isolated in a field near Arataca, Bahia. Three nests are visible. Vertically oriented, pendant nest on lower left of tree is typical of an active nest. The two spherical, nest-like structures built around limbs are superficially similar to nests of *Acrobatornis*.

dropped at least some of their leaves in October, made it easier to see nests in them than in many other trees. To test this, we searched carefully in various kinds of trees shading cocoa and presented tape playback of *A. fonsecai* in parts of the serra Bonita where no nests were obvious. This effort resulted, however, in the location of only one nest tree, which turned out to be a *Schizolobium parahyba* (Leguminosae).

We were able to collect two of five nests in a *Senna multijuga* tree (Figs. 1, 2), neither of which was active. One of these, shown in Fig. 4, was damaged on removal from the tree, having lost a horizontal (roughly

FIG. 4. Nest of *Acrobatornis fonsecai* removed from nest tree shown in Figs. 1 and 2. This nest is missing the entrance tunnel, but shows the single, moss-lined chamber with its covering of twigs and sticks.

in the same line as the main axis of the nest) antechamber or entrance tunnel of undetermined length. We noted such entrance tunnels on all four active nests located, and numerous other nests, and concluded that it is a typical feature of active nests of *A. fonsecai.* Entrance tunnels were always toward one end of the nest, usually the lower end if the orientation of the nest was other than horizontal. Bearing in mind that description of most aspects of the external, stick-structure of this nest are rendered somewhat inaccurate because an undetermined number of sticks was lost, we present the following observations.

The outer layer, which was made up entirely of a dense weave (lining materials not visible) of sticks, none of which had thorns or spines, measured 18 cm long, about 24 cm in diameter (across the center of the chamber), and 18 cm tall or deep, not including sticks extending out irregularly from the main body. We dismantled the nest for more detailed analysis of its architecture. It contained 374 sticks (total mass 115 g) ranging 1 to 3 mm in diameter, which we separated into three classes by length: 10–15 cm (276; 74% of number, 50% of mass); 15–20 cm (75; 20% of number, 32% of mass); and over 20 cm (23; 6% of number, 18% of mass). The longest and thickest sticks, all of which were around the

FIG. 5. Nest-like structure of *Acrobatornis fonsecai,* built around the fork of a rather heavy branch, with no entrance or chamber, and with an *Epiphyllum* sp. cactus growing out of it. This structure contained several small ant nests. We suspect that such nest-like structures, or "extra nests" of *Acrobatornis* might serve as dummy or cock nests, or as stores of sticks and building foundations.

outside edge, were 27 cm long and 3 mm in diameter (N = 4). These sticks seemed light in weight relative to their length, varying from 0.8–1.2 g.; the heaviest equaled about 8.5% of the body weight of the bird (about 14 g.).

Beneath the external layer of sticks was a dense lining, 18 cm in diameter (thus 75% of the total width of the nest) and about 10 cm deep, with a mass of about 85 g. It was made up primarily (about 70%) of one type of moss, most of which appeared to be healthy and green when collected, and even when the nest was dismantled in February 1996. Also

woven into this layer were rachises of decomposed leaves, which were more numerous around the incubation chamber. The chamber was quite rounded, and measured about 6 × 6 cm. Concentrated around it were pieces of *Tillandsia usneoides* lichens and *Marasmius* sp. fungus (see Sick 1957). One convoluted strand of the latter measured 90 cm. The chamber was surrounded with one type of leaf, which seemed to be a species of bamboo or bamboo-like grass. These leaves were folded or wrapped around the walls of the chamber, and averaged 12 cm long and about 2.5 cm wide. Some of the leaves had flecks of bird droppings on them. Because this nest was not active at the time of collection, it is possible that other birds or mammals had modified the interiormost lining materials.

Some nests are considerably longer (thus, more rectangular in profile) than others, which we suspect is owing mostly to variation in length of the entrance tunnel. This variation was not great relative to variation in the dimensions of the stick-nests of some other furnariids, as in some species of *Phacellodomus, Pseudoseisura,* and *Asthenes* species (pers. observ.), and we estimated the largest nest we saw to be about 45 cm long and of average circumference.

Our limited observations suggest that only one nest per tree is active at one time. This is reported to be the case with *Phacellodomus rufifrons,* which often has multiple nests in a single tree (Thomas 1983; Fig. 3). A variety of furnariids are known to build substantial stick-nests (Vaurie 1980, Narosky et al. 1983) that may persist with little external damage for months or even years (e.g., Skutch 1969, Nores and Nores 1994, various taxa pers. observ.). Thus, it seems likely that some of the "extra" nests of *Acrobatornis fonsecai* in multiple-nest trees are old nests.

Does Acrobatornis *build dummy or cock nests*?—A number of observations suggest that *A. fonsecai* may frequently construct one or more dummy or cock nests in trees with an active nest. Of two nests collected, the one described above appeared to be a true or complete nest, with a single, well-lined chamber occupying most internal space of the nest. It was not active when collected, but the fact that it was lined, and had traces of old bird droppings on some of the lining material, may indicate that it was at one time an incubation nest rather than a dormitory or dummy nest (Skutch 1969a). The other nest, although quite similar in overall size, shape, and external composition to the true nest, had no sign of an entrance or internal chamber; it was simply an oblong ball of sticks in a fork of a branch with one part of the branch through the middle of it, thus, not an old nest or a potential dormitory (Fig. 5). This nest had an epiphytic cactus (*Epiphyllum* sp.) growing out of it in several directions, which we suspect had formed the original foundation for construction, and there were several small ant nests within it. In the orientation

in which it was in the tree (similar to that in Fig. 5), it measured 32 cm high, 22 cm wide, and 16 cm deep. Relative to the other nest, this chamberless one was constructed of shorter sticks.

A third nest from this same tree fell apart when detached from its supporting limb. We could not, therefore, examine it in detail, but we determined that it contained no lining, and suspect that it had no internal chamber. We noted on many occasions that "nests" in multi-nest trees showed appreciable variation in size, with the smallest ones often too small to have an internal chamber.

We have one more, rather fascinating observation relating to the possible deployment of dummy nests by *A. fonsecai.* We observed that one of four nests in a single tree near Camacan was actually a small, arboreal ant nest that had been decorated with twigs, resulting in its remarkable similarity to the other three *Acrobatornis* nests in the tree. It seemed to us that the sticks had been applied evenly and loosely in a horizontal orientation, after the ant nest was in place, and not left over after an interior occupation and outward construction by the ants that resulted in a uniform distribution of sticks. It also seems almost unimaginable to us that the birds had perceived that the ant nest was similar in size and shape to their own nests, then added some sticks to make it a dummy. It is perhaps more likely that they started adding twigs to the stable substrate of the ant nest, and built around it to some extent. Regardless of the birds' "intent," it fooled us for a few moments.

We suggest that the normal-sized but chamberless nest (Fig. 5), the "customized" ant nest, and small, probably chamberless nest-like structures in multi-nest trees, serve as dummies that may confuse predators as to the location of the true nest. Such a function has been attributed to dummy nests atop true nests constructed by pairs of Barred Waxbills (*Estrilda astrild*).

The multi-chambered stick nest of *Phacellodomus rufifrons* may contain dormitories and an incubation chamber or, if not the active nest, just dormitories, but they apparently always have internal chambers (Skutch 1969, Thomas 1983). Skutch (1969) believed that the complexity of nests of *P. rufifrons* made it difficult for predators (and even him) to locate the eggs and young within, and he proposed that complex construction was not only designed to confuse predators but also represented "an outlet for excess energy or a pastime."

Although neither of the above authors suggested that the multiplicity of nests of *P. rufifrons* in a single tree might confuse predators (or nest parasites like *Tapera naevia,* the Striped Cuckoo), looking for eggs, young, or adults, we suspect that this could contribute an important advantage for thornbirds' survivorship. The same reasoning applies equally

well to explain the fact that *Acrobatornis fonsecai* often has more than one nest or nest-like structure in a tree. Even if non-active nests are assumed or eventually proven to be nests previously used by the birds as incubation chambers or dormitories, the fact remains that the birds repeatedly select the same tree for nest construction, one reasonable consequence of which is confusion of predators.

Another, non-exclusive, explanation for the construction of more than one nest in a single (presumably especially desirable) tree might be that "extra nests" represent resource stores (i.e., building materials and construction foundations). Sticks take a great deal of time and energy to gather and transport, and are a valuable enough resource that they are pirated by conspecifics in some species (Skutch 1969, Thomas 1983), or even other, unrelated species (pers. observ.). Furthermore, a wide variety of birds (conspecifics and others) are known to take advantage of old stick nests for construction materials or in their entirety, for nesting. We observed *Phacellodomus rufifrons* stealing sticks from a nest of *Acrobatornis fonsecai*; we noted no interspecific interaction, and we were unable to determine whether the nest of the latter was active at the time. Extra nests of *Acrobatornis,* many of which are smaller than active nests, might also secure foundation sites, ensuring the rapid construction of a nest should the primary one be lost or damaged. Thomas (1983) pointed out that the most difficult and energy-expensive stage of nest construction for *Phacellodomus rufifrons* was, by far, the establishment of a foundation.

Does Acrobatornis have "helper" offspring?—In early October, we observed many *Acrobatornis fonsecai* occupied principally with feeding young (see Pacheco et al. 1996), and we observed nest-building or maintenance behavior on only one occasion. Late on the afternoon of 11 October we saw three of four *A. fonsecai* remove sticks, one at a time, from a single nest in a densely foliated tree and carry them to another, slightly taller, leafless tree about 40 m away that contained two nests. Two adult birds and one of two brown, immature birds each carried one stick. The birds took sticks in the bill near the midpoint and, flying rather laboriously with the neck craned upwards, landed on the nest under construction. After clambering around on the top and sides of the nest for a moment with the stick, they deftly placed it in the upper exterior of the nest. We do not know how sticks are originally gathered (i.e., from the ground or by breaking them off trees) but, among furnariids, reuse of sticks from old nests or nests of other species has been reported by Skutch (1969) and Thomas (1983) for *Phacellodomus rufifrons,* and for *Pseudoseisura lophotes* by Nores and Nores (1994).

The observation of an immature bird involved in construction of a nest

where adults were also building seems to be rare within the Furnariidae. Such "helping" behavior of presumed offspring has been previously reported for *Phacellodomus rufifrons* by Gilliard (1959) and Skutch (1969), although Thomas (1983) judged that the contribution of young thornbirds to nest construction and maintenance was "minimal." Additionally, Nores and Nores (1994) found that young *Pseudoseisura lophotes* performed a low level of helping in nest construction. Because few studies sufficiently detailed to reveal this kind of behavior have been conducted on furnariids, it is perhaps not surprising that there have been so few reports of young helping parents in construction of nests. In the case of *Acrobatornis fonsecai,* in which adults and immatures (juveniles, at least) are strikingly dichromatic, a most unusual condition in the Furnariidae, it would be relatively easy to conduct further observations to determine to what extent immatures (and, if color-banded, offspring) assist in nest-building or other activities.

Brown (1987) included *Phacellodomus rufifrons* in a list of species (his table 2.2) having helpers at the nest, citing Skutch (1969) and Thomas (1983). He defined a helper as "an individual that performs parent-like behavior toward young that are not genetically its own offspring." However, the accounts of helping in Skutch (1969) and Thomas (1983) document only that presumed young birds occasionally help parents in nest construction or maintenance. *Phacellodomus rufifrons,* as presently known, then, does not fit Brown's (1987) definition of a helper and should be removed from his table 2.2. Consequently, no member of Furnariidae is known to have a helper. On the morning of 11 October, Barth saw an immature (brown-plumaged) *Acrobatornis fonsecai* feed an insect to a food-begging juvenile being fed occasionally by a pair of adults. The four birds probably formed a family group. This observation of apparent helping (sensu Brown 1987; no pun intended) is intriguing, and merits further investigation.

The extra, possibly dummy nests of *Acrobatornis,* without entrances or chambers, if proven to be typical, might be a simpler, primitive form of false nest, with more complex, derived, dummy nests of some other birds (e.g., *Phacellodomus rufifrons,* some Troglodytidae) having evolved to serve as dormitories as well. It seems worthwhile to advance the possibility, in other words, that these nest-like structures represent the ancestral, least-complex state, the derived state of which is dummy nests that have false chambers that may or may not serve as dormitories. One apparent problem with this idea is that dummy nests have not been reported for other furnariids (or other suboscines?). We suggest, however, that extra thornbird nests within a single tree or, in the case of very large nests such as those of *Pseudoseisura* species, perhaps even in nearby trees, could be

dummy nests (i.e., construction of dummy nests might have been misinterpreted to a large extent). Interestingly, neither Skutch (1969), Thomas (1983), or Nores and Nores (1994) advanced any explanation for multiple stick-nests in a tree, apparently assuming that these were all old nests or (in the case of Skutch) the result of excess energy. Another problem is that chamberless "nests," whether dummies or not, are apparently unreported in birds. Thus, the theory that *Acrobatornis fonsecai* might be using such structures as dummy nests or resource stores (as described earlier) is novel and, of course, untested.

Intrafamilial comparison of nest architecture.—Genera and species here compared with *Acrobatornis fonsecai* are the same discussed by Pacheco et al. (1996) for comparisons of morphology, vocalizations, and behavior.

Cranioleuca.—Nests (apparently only one per tree) are generally 25–30 cm in diameter, and are single-chambered, globular or conical masses of moss, grass, thin vines, and other flexible vegetation, in some species pendant from limbs at the periphery of trees, in others placed in a fork of branches or network of supporting vines and other vegetation. *Cranioleuca pyrrhophia* (Stripe-crowned Spinetail, of semiarid scrub and woodland in Bolivia, Paraguay, and northern Argentina), however, builds a nest of dry, thorny twigs bound with wool and vegetable fiber, and well-lined with lichen, or other soft material (Hoy *in* Vaurie 1980), or of soft vegetable material with a covering of sticks, in some cases spiny ones (Narosky et al. 1983). Reports differ regarding the location of the entrance (near the top or the bottom), and there is apparently no entrance tunnel.

Asthenes.—In comparing nests of *Asthenes* species with that of *Acrobatornis fonsecai,* we follow Pacheco et al. (1996) in limiting discussion to the "stick-nesting" group of *Asthenes.* Typical nests (usually one, occasionally two or three, per tree/shrub) are masses of twigs and sticks roughly 20–40 cm in diameter with single internal chambers built, for example, inside the crown of a tree or shrub, around the arms and trunk of columnar cacti, or within piles of rocks or in vegetation clinging to cliffsides. Some, such as *A. patagonica* (Patagonian Canastero), have entrance tunnels as long as the main body of the nest (Narosky et al. 1983; pers. observ.).

Thripophaga.—Both *T. macroura* (Striated Softtail) and *T. fusciceps* (Plain Softtail) construct roughly globular nests about 20 cm in diameter of small twigs and flexible vegetable material, such as grasses, rootlets, and thin vines. Nests are situated on thin limbs in the crowns of midstory and subcanopy trees, near the periphery of the tree, inside or at the edge of tall forest. We have seen only two nests of each species, however, and have examined none in detail.

Phacellodomus.—Nests of most species are similar to those of *P. ruf-ifrons* shown in Fig. 3 and described in detail by Skutch (1969) and Thomas (1983). As is true of *Acrobatornis fonsecai,* there is often more than one nest/tree; active nests are usually situated at the periphery of trees, well below the crown and, as described earlier, differ from nests of *A. fonsecai* in a number of important respects.

Xenerpestes.—The two distinctive species in this genus are poorly known. Unfortunately, nests remain undescribed, although Ridgely and Gwynne (1989) suspected that a large stick-nest in eastern Panama belonged to the Double-banded Graytail (*X. minlosi*). Whitney observed a pair of *X. minlosi* hopping on a mass of twigs and sticks about 20 cm in diameter that he suspected was their nest, in the crown of a tall, foliated and flowering *Erythrina* tree at the Cana airstrip, Darién, Panama, in January 1992.

Metopothrix.—The sole member of *Metopothrix, M. aurantiacus* (Orange-fronted Plushcrown), like *Xenerpestes,* is poorly known. Nests were briefly described by Ridgely and Tudor (1994:128) as masses of sticks nearly 0.5 m across with the entrance at the side, built on lateral branches of trees from 4 to 20 m above ground, "not dissimilar in overall form from those of *Phacellodomus* thornbirds." These authors stated that Fraga (1992) had previously "described just such a nest" of *Metopothrix,* but Fraga's paper indicates that he saw birds carrying sticks only; he did not observe or describe a nest. *Metopothrix* nests are apparently considerably larger than those of *Acrobatornis* and are sometimes placed much nearer the ground; details of construction remain unknown.

Margarornis.—The only descriptions of the nest of any species appear to be those of Hilty and Brown (1986:367) and Fjeldså and Krabbe (1990: 384) for *M. squamiger* (Pearled Treerunner): "moss ball nest with side entrance" and "closed nest of moss, placed under a limb or a rock," respectively. In exterior architecture and general size and shape, nests of "stick-nesting" *Asthenes* are much like nests of *Acrobatornis fonsecai,* and appear to be the most similar in the family. *Cranioleuca pyrrhophia*'s construction of sticks around a well-lined chamber recalls that of *A. fonsecai.* This seems to be the only described stick-nest of that genus, although Whitney has recently discovered that *C. meulleri* (Scaled Spinetail) of the lower Amazon region, also builds an arboreal stick-nest (ms. in prep.). *Cranioleuca pyrrhophia* lives in habitats with little or no moss or flexible, herbaceous growth suitable for structural binding (or at least no reliable sources of such materials), which may have promoted stick-nesting (or the maintenance of it) in this species. We suspect, however, that the single-chambered, mossy globes of some of the other *Cranioleuca* species would be quite similar to nests of *Acrobatornis* if covered with a

layer of sticks. Just as sticks are abundant and easily accessible in the habitat of *C. pyrrhophia,* they are relatively rare (i.e., soft, hard to break off, and decompose quickly on the ground) in the humid montane habitats of most of the other members of the genus. We await documentation and detailed descriptions of the nests of the two species of *Xenerpestes,* and of *Metopothrix aurantiacus.*

On the origin of stick-nesting in Furnariidae.—There appears to be no published discussion of the origin of stick-nesting in Furnariidae. We suspect that powerful environmental factors in place for prolonged periods would be required for evolution and establishment of such energetically expensive, sex-shared (i.e., nests are not sexually selected structures), nest architecture across the broad group of furnariids in which the behavior is prevalent today. During arid or semi-arid epochs, for example, there may have been few other construction materials available. Extended periods of winds, frequent violent weather, or cold would represent substantial selective forces. Similarly, fortified nests might have evolved to thwart large reptilian and avian predators and to withstand the shock of regular, incidental contact of nests and supporting vegetation by large vertebrates. Operative evolutionary mechanisms aside, we assume that the ancestral forms of stick-nesting furnariids arose in a southern, Chaco-Patagonian/Pantanal (in contemporary terms) distributional center during a pre-Andean epoch. In light of the overwhelming concentration and diversity of stick-nesting species surviving in this region of the continent today, origin of stick-nesting there is a reasonable assumption. This ancient center probably extended to interior northeastern Brazil, which today shares numerous forms with Chaco-northern Patagonia and the Pantanal (Short 1975 and numerous subsequent authors), including such stick-nesting furnariids as the Chotoy Spinetail (*Schoeniophylax phryganophila*), *Phacellodomus rufifrons,* Firewood-gatherer (*Anumbius annumbi*), and Rufous Cacholote (*Pseudoseisura cristata*). The contemporary distribution of stick-nesting *Asthenes* reaches its northeastern extreme only slightly farther south, in the serras of Minas Gerais (*A. luizae* Cipo Canastero). Certain successful forms apparently radiated widely (e.g., *Phacellodomus rufifrons* and *Anumbius,* which are still spreading, following forest clearance), and some, like stick-nesting *Asthenes,* speciated rapidly as they colonized a new, vertical stratum of Andean habitats to spread north to central Peru, where speciation seems relatively incipient. Forest-inhabiting *Cranioleuca* may have radiated following evolution of a more recent ancestral form in the forests that must have flourished with the condensation-precipitation (at least) resulting from Andean uplift. Such a sequence of events implies that stick-nesting is the primitive condition in this group of birds, at least.

ACKNOWLEDGMENTS

We are grateful to Haroldo C. de Lima of the Botanical Garden of Rio de Janeiro for determining the species of one of the nest trees from dried samples we provided. Claudia Bauer and Luiz Gonzaga helped in analysis of nest architecture of *A. fonsecai.* We thank Hannah Gould of the Univ. of Texas at Austin for helping us locate pertinent references. Gary Graves and J. V. Remsen, Jr. commented on the manuscript, and Charles Blem assisted in seeing that it was published promptly. Holland Photo of Austin produced the black-and-white photos in the figures. Field Guides Incorporated, of Austin, Texas, generously financed part of our expenses for research in southern Bahia.

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Wilson Bull., 108(3), 1996, pp. 449–456

WOODPECKER EXCAVATION AND USE OF CAVITIES IN POLYSTYRENE SNAGS

Richard N. Conner and Daniel Saenz

Abstract.—We examined woodpecker excavation and use of artificial polystyrene snags in four forest types in eastern Texas for five years. Twenty-three of 47 artificial snags were used by Downy Woodpeckers (*Picoides pubescens*) for cavity excavation and subsequent nocturnal roosting; they did not use the artificial snags for nesting. Although six other species of woodpeckers were present in the area, only Downy Woodpeckers excavated cavities in the artificial cavity substrate. Entrances to cavities in artificial snags became enlarged within several months of excavation. Other wildlife species using abandoned cavities in artificial snags were Carolina Chickadees (*Parus carolinensis*), Prothonotary Warblers (*Protonotaria citrea*), southern flying squirrels (*Glaucomys volans*), and red wasps (*Polistes* sp.). In one instance, Carolina Chickadees excavated their own cavity and nested within a polystyrene snag. Until an artificial cavity substrate acceptable for both woodpecker excavation and nesting can be found, the utility of artificial snags as a means to augment woodpecker nesting substrate remains inadequate. *Received 18 October 1995, accepted 16 January 1996.*

Many woodpecker species and secondary cavity nesters depend on snags (standing dead trees) for cavity sites that they use for nesting and roosting (Conner 1978, Evans and Conner 1979, Thomas et al. 1979, Raphael and White 1984). Harvesting of mature forests can greatly reduce the availability of substrate for woodpeckers to excavate nest cavities (Conner 1978, Dickson et al. 1983). Thus, artificial cavity substrate may benefit nesting woodpeckers in areas where snag availability is low.

Peterson and Grubb (1983) evaluated woodpecker use of 50 artificial polystyrene snags (242-cm high × 22-cm diameter) over an 11-month period in Ohio. Downy Woodpeckers (*Picoides pubescens*) excavated 51 cavities in 42 of the snags, used them for nocturnal roosting, but failed to use the cavities for nesting. House Wrens (*Troglodytes aedon*) and Carolina Chickadees (*Parus carolinensis*) nested in cavities excavated by Downy Woodpeckers. Peterson and Grubb (1983) speculated that other larger species of woodpeckers might use polystyrene snags if snags >22-cm diameter were provided, but this idea has never been tested. Artificial polystyrene snags have also been used to explore sexual differences in selection of cavity sites by Downy Woodpeckers and to evaluate cavity entrance orientation and snag selection relative to vegetation in a regenerating clear cut (Grubb 1982, Petit et al. 1985).

We evaluated woodpecker use of 26-cm diameter × 242-cm high poly-

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TABLE 1

VEGETATIONAL CHARACTERISTICS (MEANS ± SD) OF MATURE PURE PINE, PINE-HARDWOOD, UPLAND HARDWOOD, AND BOTTOMLAND HARDWOOD FOREST STANDS WHERE ARTIFICIAL POLYSTYRENE SNAGS WERE STUDIED ON THE STEPHEN F. AUSTIN EXPERIMENTAL FOREST IN EASTERN TEXAS

Vegetation variable	Pure pine (N = 20)	Pine-hardwood (N = 20)	Upland hardwood (N = 20)	Bottomland hardwood (N = 20)
Vegetation height (m)	30.0 (3.7)	27.4 (5.5)	20.6 (2.9)	27.1 (5.3)
Pine basal area (m^2/ha)	23.5 (3.9)	22.6 (7.3)	3.8 (3.6)	0.2 (0.5)
Hardwood basal area (m^2/ha)	0.2 (0.6)	4.0 (3.2)	15.6 (3.5)	18.5 (4.8)
Tree density (#/0.04 ha)	11.5 (3.6)	18.5 (9.6)	10.1 (3.2)	14.0 (3.6)
Canopy closure (%)	73.1 (11.1)	71.2 (14.3)	69.3 (13.8)	72.5 (13.0)
Ground cover (%)	2.9 (2.8)	3.5 (2.4)	3.5 (2.7)	9.6 (6.4)
Natural snags (#/0.04 ha)	0.8 (0.8)	0.7 (0.9)	0.7 (0.8)	1.1 (1.0)

styrene snags in four forest types over a five-year period. We determined secondary cavity nester use of woodpecker cavities and evaluated cavity shape and condition with long-term use.

STUDY AREAS AND METHODS

We constructed 47 artificial snags from solid blocks of polystyrene (26-cm diameter × 242-cm high). The 4-cm increase in diameter of the polystyrene snags above what had been used previously (Peterson and Grubb 1983), placed the substrate diameter within the range of sizes used by Hairy (*Picoides villosus*) and Red-bellied (*Melanerpes carolinus*) woodpeckers for cavity sites (Conner 1978). Similar to Peterson and Grubb (1983), we painted the artificial snags with a thick coating of brown latex paint to enhance the snag-like appearance of the polystyrene snags. After drilling a centrally located 3-cm diameter hole (parallel to the length of the snag), 80 cm deep into the base of each artificial snag, we installed it in the field on 20 October 1986 by sliding it onto a 184-cm long "T-pole" (iron fence post) that had been driven into the ground approximately 110 cm deep. The hole drilled into the base of each artificial snag was made solely to mount (impale) the snags on T-poles. All artificial snags were installed as close to vertical as possible, i.e., no lean could be visually detected. Artificial snags were installed at 112-m intervals on four nest box trails in four forest types (ten snags per trail and one trail in each forest type: mature pure pine [*Pinus* spp.], pine-hardwood, upland hardwood, and bottomland hardwood forest habitats) located on the Stephen F. Austin Experimental Forest (31°29′N, 94°47′W) in southern Nacogdoches County, Texas. Each nest box trail was circular and approximately 1130 m in length. Cavities for secondary cavity nesters were readily available on each trail, because 20 sites with three nest boxes per site were established at 56-m intervals on each trail as a part of a different study. Seven additional artificial snags were installed on the edge of mature pine-hardwood forest next to dirt roads.

Vegetation characteristics were measured at 56-m intervals (20 points) on each of the four nest box trails (Table 1). We measured vegetation height with a clinometer, and tree basal areas were measured with a one-factor metric prism. Densities of trees and snags >15 cm diameter at breast height were counted within an 11.3-m radius circular plot. We esti-

TABLE 2

SPECIES USE OF CAVITIES EXCAVATED BY DOWNY WOODPECKERS IN ARTIFICIAL POLYSTYRENE SNAGS IN FOUR FOREST TYPES ON THE STEPHEN F. AUSTIN EXPERIMENTAL FOREST IN EASTERN TEXAS

Cavity occupant	Number of polystyrene snags used			
	Pure pine (N = 10)	Pine-hardwood[a] (N = 17)	Upland hardwood (N = 10)	Bottomland hardwood (N = 10)
Downy Woodpecker[b]	0	13	10	0
Carolina Chickadee	0	4[c]	2	0
Prothonotary Warbler	0	0	2	0
Southern flying squirrel	0	1	0	0
Red wasps	0	3	2	0

[a] Artificial snags in forest (N = 10) and edge (N = 7) pine-hardwood habitat combined.
[b] All cavities except one were initially excavated by Downy Woodpeckers.
[c] In one instance in pine-hardwood edge habitat Carolina Chickadees excavated their own cavity.

mated percent canopy closure and ground cover, using a 4-cm diameter × 12-cm long hollow tube. We recorded height and compass aspect of pecking and cavity excavation on all artificial snags from fall 1986 to summer 1991.

Occupants of cavities were determined by checking roosts with a mirror, watching occupants use a cavity, or flushing the occupant. Artificial snags were visited during the spring (March–May), fall (September–October), and winter (December–January) during each year of the study. The species of woodpeckers excavating cavities in artificial snags were determined by watching the actual excavation or by measuring the final size of the completed cavity. We also noted claw marks and their relative size to determine if they had been made by a squirrel or a possible predator (house cat [*Felis domesticus*] and raccoon [*Procyon lotor*]). We were not able to determine nesting success on all of the avian nests detected because of time and personnel constraints. Artificial snags in the bottomland hardwood area were monitored only until spring 1989 because flooding lifted the snags off the T-poles and washed them down the Angelina River.

RESULTS

Except for one case, Downy Woodpeckers were the only species detected excavating and using cavities in the artificial polystyrene snags (Table 2). We did not observe Downy Woodpeckers nesting in any of the cavities, but they regularly used the cavities as nocturnal roosts. Downy Woodpeckers excavated cavities in artificial snags only in the pine-hardwood and upland hardwood forest types. Carolina Chickadees were the most frequent secondary users of cavities excavated by Downy Woodpeckers (Table 2). In one instance, Carolina Chickadees excavated a cavity during the early spring and successfully nested in it. Prothonotary Warblers (*Protonotaria citrea*) successfully nested in two different cavities in the upland hardwood forest type. Standing water was present in parts of this area for much of the spring. Five cavities were used by red

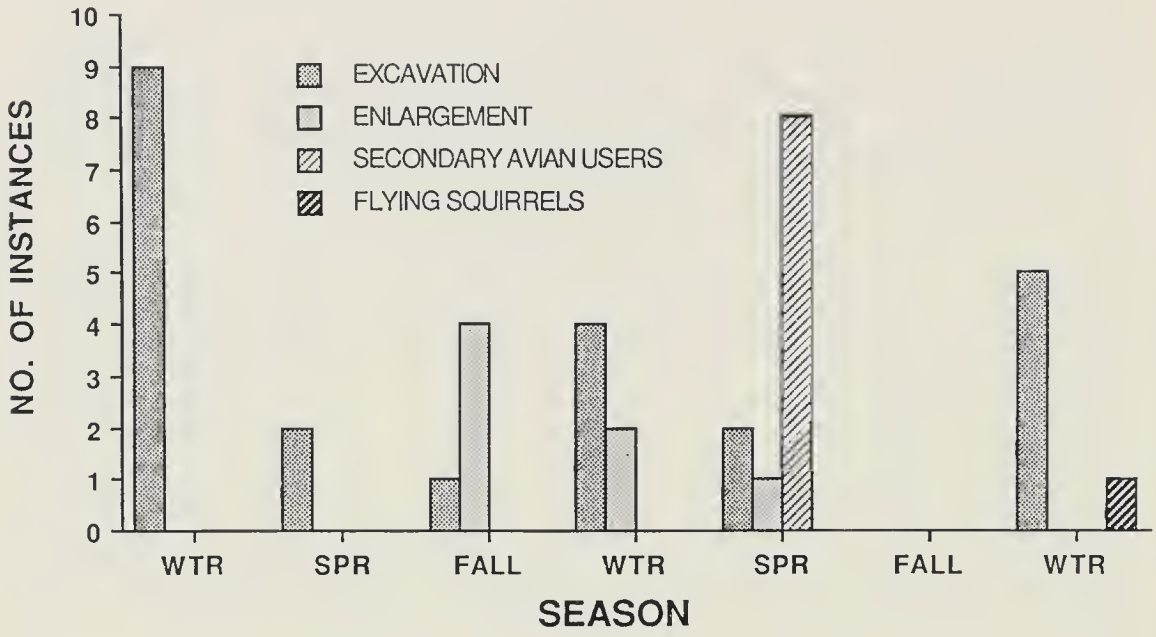

FIG. 1. Seasonal appearance of cavities completed by Downy Woodpeckers in polystyrene snags (starting in winter 15 months after snag installation), enlargement of cavities by subsequent use, and use by secondary cavity users during successive winter (WTR), spring (SPR), and fall (FALL) seasons on the Stephen F. Austin Experimental Forest in eastern Texas.

wasps (*Polistes* sp.) and one by southern flying squirrels (*Glaucomys volans*).

Artificial snags were in place five months before small holes began to appear in them in the upland hardwood and pine-hardwood areas during the early spring 1987. Downy Woodpeckers were the only woodpecker species observed excavating cavities in the artificial snags, and the first completed cavities (9) appeared in these two habitat types by early January 1988 (15 months after installation) indicating that they had been excavated during late fall to early winter 1987. Additional completions of cavities in other artificial snags occurred during the next two years (Fig. 1). Avian secondary cavity nesters did not begin to use the completed cavities until more than a year had passed (Fig. 1). Southern flying squirrels were first detected after two years.

All completed cavity entrances were excavated between 12 and 16 cm from the top of the artificial snags. It was difficult to detect visually a preference for cavity orientation. Cavity entrances appeared to be bimodal in their distribution (Fig. 2). A Rao's test indicated a non-random orientation of entrances ($U = 1{,}591$; $P < 0.01$).

Small holes that seemed to be similar to cavity starts appeared near the tops of two artificial snags in the pure pine area within five months of snag installation. Cavities in those two snags, however, were never com-

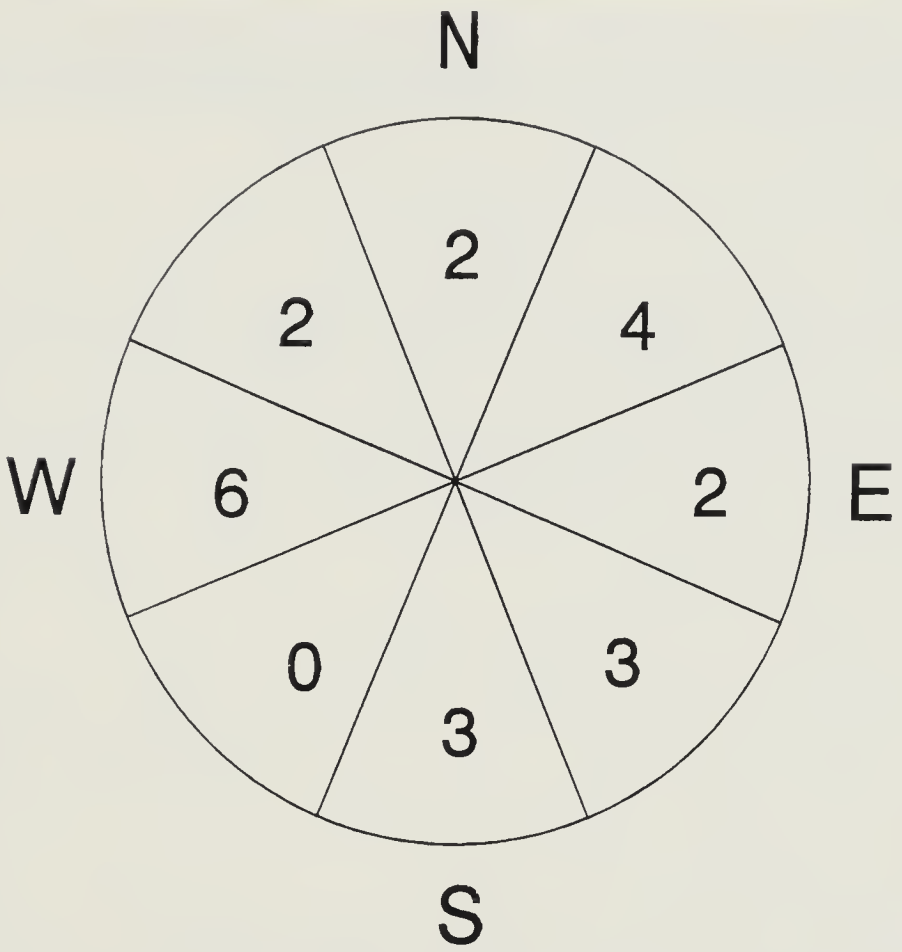

FIG. 2. Aspects of entrances to cavities excavated into artificial polystyrene snags (N = 22) in eastern Texas.

pleted. By January 1988, two other artificial snags in the pure pine area had small excavations in them but were also abandoned. Artificial snags in the bottomland hardwood area had small and some large holes excavated within 30 cm of the base of the snags, most likely excavated by Pileated Woodpeckers (*Dryocopus pileatus*). But, apparent start holes in both the pure pine and bottomland hardwood areas were never excavated beyond several centimeters deep. Artificial snags in all areas had varying amounts of their surface paint and polystyrene pecked away, as if woodpeckers or other bark foragers had attempted to forage on them.

Seven cavity entrances became quite enlarged within 8–10 months following cavity completion and subsequent use (Fig. 1). Although entrances enlarged in all directions, the bottom of each entrance was affected the most. Polystyrene would erode away 10–15 cm, most likely during the passage of the occupant, so that entrances gradually became elongated vertically. Downy Woodpeckers appeared to abandon enlarged cavities.

Claw marks of sufficient size to suggest attempted predation appeared on four of the artificial snags with cavities during the fall and winter. In one instance, the cavity entrance was torn open and about half of the cavity chamber exposed.

DISCUSSION

Our attempt to use large diameter polystyrene snags to encourage some of the larger woodpeckers to excavate cavities was unsuccessful. Although both Red-bellied and Hairy woodpeckers were present within the vicinity, neither species apparently excavated cavities in the artificial snags. Diameters of the artificial snags were sufficient to house cavities made by these two species (Conner et al. 1975, Jackson 1976). However, the 3-m height of the artificial snags, which was the tallest block of polystyrene commercially available, may have been too low for these two species. Hairy and Red-bellied woodpeckers typically excavate nest cavities at heights above 3 m (Conner 1978). Downy Woodpeckers often nest in dead tree stubs that are approximately 3 m in height (Conner et al. 1975). They also are known to excavate cavities in very soft, well-decayed natural snags (Conner et al. 1975, 1976). The consistency of polystyrene is very similar to that of well-decayed wood tissue found in some snags used by Downy Woodpeckers for cavity excavation. Both the polystyrene and well-decayed wood tissue can be easily excavated by a human finger nail. Substrate of such little structural strength may be too soft for the larger woodpecker species.

Although there were woodpeckers within the pure pine and bottomland hardwood study areas, none of the polystyrene snags in these study areas was used for cavity excavation. There was an abundance of natural snags in the bottomland habitat (Conner et al. 1994, Table 1); thus, the attractiveness of artificial snags was likely less. Natural snags were as common in the pure pine stand as they were in the pine-hardwood study area (Table 1). The failure of Downy Woodpeckers to use artificial snags in the pure pine stand is enigmatic.

The long term value of polystyrene snags as an artificial substrate for woodpecker cavity excavation appears to be relatively low. Only Downy Woodpeckers excavated cavities, and they did not nest in the cavities following excavation. The artificial snags do appear to have some value as roosting sites for Downy Woodpeckers, and the polystyrene material is well known for its high insulating ability, which would be particularly valuable during winter at northern latitudes. Although woodpeckers did not use the cavities for nesting, secondary cavity nesters such as Prothonotary Warblers and Carolina Chickadees successfully nested in the artificial substrate. Entrances to cavities, however, soon begin to erode

away with use, rendering the cavity unusable after several years. This problem could be rectified by reinforcing cavity entrances with wire mesh or thin wood following the woodpecker's completion of the cavity chamber.

Still, artificial substrates for woodpecker cavity excavation may have value. Substrates with a stronger yet brittle structure may be needed to entice other woodpecker species to excavate cavities and Downy Woodpeckers to nest. Also, additional structure strength or hardness is needed on the surface of the artificial snags. Such strength might help deter predators and provide sufficient hardness and resonance for mutual tapping behavior and drumming which occur during cavity site selection (Kilham 1958, 1983). Also, further study using larger diameter and taller artificial snags in areas where natural snags are limited or absent may provide additional insight.

ACKNOWLEDGMENTS

We thank T. C. Grubb, Jr., D. R. Petit, and J. R. Walters for constructive comments on an early draft of the manuscript.

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Wilson Bull., 108(3), 1996, pp. 457–466

NESTING SUCCESS OF THE PROTHONOTARY WARBLER IN THE UPPER MISSISSIPPI RIVER BOTTOMLANDS

David J. Flaspohler

Abstract.—In 1993 and 1994, I studied the breeding biology and nesting success of Prothonotary Warblers (*Protonotaria citrea*) at the margin of the species' breeding range on the upper Mississippi and Black rivers in west-central Wisconsin. During the severe flooding of 1993, nesting success was reduced to a third of the level recorded in 1994, a more typical year. The rate of Brown-headed Cowbird (*Molothrus ater*) parasitism was the highest (26.9%) yet reported. House Wrens (*Troglodytes aedon*) were observed destroying only one nest, but they were suspected of having a larger role in nest failure as has been found in other studies (Walkinshaw 1938). *Received 30 Mar. 1995, accepted 21 Sept. 1995.*

The Prothonotary Warbler (*Protonotaria citrea*) is a secondary cavity nester that breeds in floodplain forests of the eastern U.S. Between 1966 and 1987, it experienced regional population declines in the southern U.S. (James et al. 1991) and in the northern Midwest (Graber et al. 1983). It is listed as one of ten area-sensitive warbler species (subfamily *Parulinae*) (Robbins 1979). Much of its floodplain forest habitat has been lost or degraded since presettlement times (Fredrickson 1979), and mangrove and riparian forests of Latin America used by the Prothonotary during the non-breeding season (Skutch 1989) are being rapidly destroyed or converted to other uses (Terborgh 1989). In the center of its breeding range in the southern U.S., less than 25% of the original bottomland forest remains (Fredrickson 1979, Harris et al. 1984). In Wisconsin, only 8% of presettlement floodplain forest remains in moderate to high quality condition (Mossman 1988).

Population monitoring of the Prothonotary Warbler across its breeding range is hampered by the inaccessibility of bottomland forests. In Wisconsin, where this study was conducted, there has been only one occurrence of a Prothonotary Warbler on all Breeding Bird Survey (BBS) routes from 1966 to 1991 (USFWS, unpubl. data), even though the species breeds commonly in suitable habitat (Mossman 1988). Furthermore, brood parasitism by the Brown-headed Cowbird (*Molothrus ater*) may be contributing to population declines by reducing productivity.

Several studies have examined the nesting ecology of the Prothonotary Warbler (Walkinshaw 1938, 1939, 1941, 1953; Petit 1986, 1989; Blem and Blem 1991, 1992). However, the majority of nests in these studies were built in artificial nest boxes. Use of artificial nest boxes may affect

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breeding parameters such as clutch size and nesting success (Mertens 1977), although preliminary studies do not support the hypothesis that nest box size affects clutch size for this species (C. Blem, pers. comm.). Hole nesting birds using nest boxes may also suffer artificially reduced rates of predation (Nilsson 1984, 1986, Moller 1989) as compared to nests in natural cavities. Conversely, the greater conspicuousness of nest boxes may increase predation rates compared to natural cavities. The diameter of a nest box entrance may also discourage or prevent cowbird parasitism. Few data exist on nesting success and brood parasitism rates for naturally occurring nests. The reproductive ecology of the Prothonotary Warbler has not been studied in detail in the upper Mississippi River region. I present here nest site characteristics, reproductive success, and rate of cowbird parasitism for Prothonotary Warblers nesting in the upper Mississippi River. This study also provides some insight into the effect of extreme flooding on the reproductive success of Prothonotary Warblers in this region.

STUDY AREA AND METHODS

I collected nesting data at three sites along a 113-km section of the Mississippi River in west central Wisconsin during 1993 and 1994 (Fig. 1) (pools 5–9, elevations 664–625′ asl, 44°09′N, 91°48′W, 43°31′N, 91°14′W). In this area, the river ranges from 1.3–4.0 km wide with numerous forested islands 0.25 to 300 ha in size. The river is bordered by steep bluffs dominated by oak forest (*Quercus* spp.) with patches of remnant prairie on steep south-facing slopes. Beyond the bluffs lie broad areas of agricultural land with scattered woodlots where there was once hardwood forest, savanna, and open prairie (Emlen et al. 1986). Riparian habitat occurs on islands and in strips 0.1 to 1.5 km wide on either shore of the river. Eastern cottonwood (*Populus deltoides*) and black willow (*Salix nigra*) are found on new alluvial deposits (Olsen and Meyer 1976). Older alluvial sites and mesic areas are dominated by silver maple (*Acer saccharinum*), green ash (*Fraxinus pennsylvanica*), river birch (*Betula nigra*), box elder (*Acer negundo*), and basswood (*Tilia americana*). American elm (*Ulmus americana*), once a dominant canopy species, is now represented only by saplings and young trees, larger trees having succumbed to Dutch Elm disease. Dominant understory plants include woodbine (*Parthenocissus inserta*), wood-nettle (*Laportea canadensis*), jewelweed (*Impatiens capensis*), violet (*Viola* spp.), poison ivy (*Rhus radicans*), button bush (*Cephalanthus occidentalis*), and grape (*Vitis* spp.) (Olsen and Meyer 1976).

Information on nesting Prothonotary Warblers was also collected at two sites along the lower portion of the Black River, two and seven km above its confluence with the Mississippi River. Floodplain vegetation along the lower Black River is similar to that on the Mississippi River (Barnes 1991). From mid-June to the end of July 1993, both the Mississippi River and the Black River experienced record-breaking floods which were directly responsible for numerous nest failures.

From mid-May to the end of July 1993 and 1994, I found nests by walking or canoeing through promising habitat and by following singing males. I recorded the location and stage of nesting along with characteristics of the nest and site. I returned to check each nest approximately every four days. I calculated nest success according to procedures in Mayfield (1961, 1975) and Caccamise (1977). Nest height was the distance from the ground to the

FIG. 1. The location of five study sites along the upper Mississippi River and the lower Black River.

bottom of the cavity opening, and only data from nests that had solid ground under them for some part of the nesting period were used (Table 1). Ratios of the number of young hatched to the number of eggs laid (H/E) and the number of chicks fledged to the number of young hatched (F/H) were used as indices of breeding success (Caccamise 1977). The Mayfield (1961, 1975) method for calculating nest success adjusts for the stage at which a nest is first discovered.

TABLE 1
NEST PARAMETERS OF PROTHONOTARY WARBLERS IN THE UPPER MISSISSIPPI RIVER BOTTOMLANDS

Parameter	1993	1994
No. nests[a]	22	20
No. eggs	90	73
No. hatched	41	23
Hatched/egg	0.46	0.32
No. fledged	25	22
Fledged/hatched	0.61	0.96
No. successful nests	10	6
Percent successful[b]	45	30
Mayfield estimate[c]	0.20	0.66

[a] Nests include only those found during egg incubation stage.
[b] Success = fledged at least one young.
[c] Success calculated using Mayfield's (1961) correction for exposure. Estimate includes all nests (1993: N = 28; 1994: N = 32) found during incubation and nestling stages and represents probability of nest surviving through both stages.

RESULTS AND DISCUSSION

The three greatest sources of mortality for eggs and nestlings during this study were flooding, predation, and destruction by House Wrens (*Troglodytes aedon*). These were also the principal sources of nest mortality in Michigan (Walkinshaw 1938, 1953). Flooding was devastating in 1993 since the "hundred year" floods coincided precisely with peak nesting activity in mid-June. In 1993, 36% of all nests were flooded, while none was lost to flooding in 1994. No nests were abandoned during this study. Increased predation rates associated with observer nest visits are unlikely, since most nests were located over water, nest visits were brief, and a variety of non-terminal routes were used when visiting a nest.

Of 43 nests for which monitoring began during the incubation period, only one was observed being destroyed by a House Wren. In this case, the House Wren punctured all four eggs in an unattended nest and dropped one into the water below the nest. It is possible, based on their abundance and aggressive habits, that House Wrens were responsible for other losses attributed to predation.

Mean clutch size (4.31, Table 2) was smaller than that reported by Petit (1989, $\bar{x}$ = 4.75, N = 120), Walkinshaw (1941, $\bar{x}$ = 5.62, N = 118), or Blem and Blem (1992, $\bar{x}$ = 4.38, N = 266). Mean tree stub diameter at nest height in this study was greater (29.9 cm) than in Petit's (1987) study (13.6 cm). Prothonotary Warblers use cavities excavated by other birds as well as naturally occurring cavities. Many nests were found in cavities

TABLE 2
CHARACTERISTICS OF PROTHONOTARY WARBLER NESTS

Characteristic	N	$\bar{X} \pm SD$
Mean clutch size[a] (eggs)	36	4.31 ± 0.79
Nest diameter opening (cm)		
Least		2.5
Greatest		9.8
Mean	74	5.0 ± 1.35
Mean nest height above ground[b] (cm)	43	219.4 ± 124.3
Mean stub diameter at nest height (cm)	76	29.9 ± 13.7

[a] Nests included are only those found during incubation.
[b] Nests from 1993 were not included because all nests were found over highly fluctuating water levels.

that had been expanded through decomposition, and these accounted for the larger diameter openings.

Prothonotary Warblers glean arthropods from the ground and shrub layer of riparian forests. While the Prothonotary Warbler is not an obligate ground forager, it does use the shrub layer extensively when foraging, and the absence of this layer during much of the 1993 breeding season may have influenced foraging efficiency.

The record-breaking floods along the Mississippi and its tributaries in 1993 were largely responsible for the lower nest success in 1993 compared with 1994. Peak flood levels occurred precisely during the height of breeding activity for Prothonotary Warblers in June. The Mississippi River near Merrick State Park, Wisconsin (Fig. 1, Sites #1, #2) rose nearly 3 m between June 16 and June 26 (U.S. Army Corps of Engineers 1993). Although no data were available on water levels at study sites on the Black River, I noted similarly dramatic rates of rise. The Prothonotary Warbler typically nests within 2–3 m of the water's surface (Harrison 1975).

Picman et al. (1993) found that nest predation near marshes decreased with increasing water depth. Unusual flood waters may have made some nests less accessible to predators, thus decreasing nest losses from predation in 1993. The percentage of nests depredated in this study (27.6%, N = 28 from 1993 only) was lower than in Walkinshaw's (1941) study (41%, N = 27) but higher than in Petit's (1989) study (20.9%, N = 191). If nests lost to flooding are removed from the pool of nests available to predators, a predation frequency similar to Walkinshaw's (1941) is generated (44.4%, N = 18 from 1993 only). No attempt was made to distinguish predation losses from other nest losses in 1994. Most of Petit's nests were in artificial nest boxes with entrance holes smaller than the

mean of the entrance holes in this study, which may have influenced predation rates in that study. Such nest box-specific effects on nest success will depend on the material used to construct the box (e.g., cardboard vs wood). House Wrens were absent from Petit's (1989) and Walkinshaw's (1941) Tennessee sites while they were common on Walkinshaw's (1941) Michigan sites and in this study. The presence of House Wrens may explain the similar predation rates for non-flooded nests in Michigan and Wisconsin, while the absence of House Wrens on the Tennessee sites may account for the lower predation rates reported by Petit (1989).

Potential nest predators observed in this study included Common Grackle (*Quiscalus quiscula*), Blue Jay (*Cyanocitta cristata*), House Wren, Common Crow (*Corvus brachyrhynchos*), gray squirrel (*Sciurus carolinensis*), and mink (*Mustela vison*). Species known to prey on Prothonotary Warbler nests include the gray squirrel (Walkinshaw 1938) and mice of the genus *Peromyscus* (Guillory 1987). Other likely predators in the study area include the raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), fox squirrel (*Sciurus niger*), and opossum (*Didelphus virginianus*). Although no snakes were seen in 1993, they were seen seven times in 1994 and have been reported as predators in other studies of Prothonotary Warblers (Petit 1989). Excluding the single nest destroyed by a House Wren, I was able to identify the predator of a nest by teeth marks in only three cases. Squirrels (*Sciurus* spp.) gnawed through the side of a total of three cavities in both live and dead trees. One such nest contained three Prothonotary Warbler eggs and five cowbird eggs and was located on a small island (<1 ha) isolated by approximately 200 m of swift and deep (>5m) floodwaters and had no dry land on it. Clearly, islands do not provide complete safety from tree-climbing terrestrial predators.

Nests were often placed in severely rotted trees in relatively exposed areas over water where they are vulnerable to damage from storms and wave action from boats. Of 76 nests in snags and stubs, none was lost due to the collapse of the tree, although two nest trees collapsed within one week after the warbler's fledging.

The incidence of cowbird parasitism was the highest yet reported (Table 3). A comparison of regional cowbird populations indicates that Midwest cowbird abundance is 2.5 times greater than in the eastern U.S. and is increasing (Robbins et al. 1986). The bottomland forests of the upper Mississippi are in agricultural lands that provide foraging habitat for cowbirds. Petit's (1989) Tennessee study was conducted in a riparian zone within a mostly forested landscape. These different land-use patterns may partly explain the higher parasitism rates in this study. Since Walkinshaw's (1938, 1941) studies in Michigan, cowbird populations have in-

TABLE 3
RATES OF COWBIRD PARASITISM OF PROTHONOTARY WARBLERS IN THE UNITED STATES

Location	No. nests	% Parasitism	Reference
Iowa	70	25.7	Norris (1890)
Michigan	28	10.7	Walkinshaw (1938)
Louisiana	57	12.3	Goertz (1977)
Illinois	154	15.6	Graber et al. (1983)
Tennessee	128	20.3	Petit (1989)
Wisconsin	67	26.9	This study (1996)
Virginia	998	0.013	Blem, unpubl. data

creased across the eastern U.S. This population increase could be partly responsible for increased parasitism rates since Walkinshaw's time.

Belles-Isles and Picman (1986) noted that House Wrens poke holes in eggs of other species within their territories, often removing the pecked eggs and disturbing the nest lining. Although I observed House Wrens destroying only one nest, Walkinshaw (1941) reported that 25% of 413 Michigan Prothonotary eggs and chicks were destroyed by House Wrens. Walkinshaw spent more time observing nesting behavior than I did during this study, giving him more opportunities to identify the cause of egg and nestling loss.

It has long been assumed that cavity-nesting birds are limited primarily by the availability of nest sites (Hilden 1965, Scott 1979, Mannan et al. 1980) and that House Wrens benefit from nest-destroying behavior by freeing up nest sites and perhaps decreasing foraging competition. Several studies have observed that Prothonotary Warblers often compete unsuccessfully for cavities with House Wrens (Smith and Dumont 1944, Graber et al. 1983). In Walkinshaw's (1941) comparative study of Prothonotary Warblers nesting in Michigan and Tennessee, he attributed comparatively lower nesting success in Michigan to competition from and nest destruction by House Wrens, a species not common on his Tennessee sites.

In a trial nest-box study conducted in 1994, we placed 20 wooden nest boxes within past Prothonotary Warbler breeding habitat. House Wrens occupied 16 (80%) of the nest boxes, and Tree Swallows (*Tachycineta bicolor*) nested in three (15%). No Prothonotary Warblers nested in the boxes.

House Wrens were the most abundant bird species in the study sites, as measured by point counts conducted during the study (Flaspohler 1994), and are common and widespread in floodplain forests throughout Wisconsin (Mossman 1988). I found numerous nests with missing eggs

and with both disturbed and undisturbed nest linings. Because of the House Wren's habit of removing nesting material from the nests that it destroys (Belles-Isles and Picman 1986), and thereby disturbing the nest, one cannot confidently conclude that a disturbed nest implies a mammalian predator as proposed by Best (1978) and Petit (1989). Where no cowbird parasitism was present, I attributed the disappearance of eggs and nestlings to predation. Where House Wrens are abundant, this method may tend to overestimate predation rates and underestimate House Wren nest destruction rates.

ACKNOWLEDGMENTS

I thank K. Goffin, S. Matteson, D. Hinebaugh, and V. Patton, for field assistance, and S. Temple, P. Arcese, M. Mossman, and D. Sample for helpful comments. Constructive reviews were provided by C. Blem, L. Petit, and an anonymous reviewer. I am grateful for a variety of logistical and material assistance provided by G. Evland of the Wisconsin Dept. of Natural Resources and E. Nelson and S. Lewis of the U.S. Fish and Wildlife Service. C. VanderVeen provided essential research support during 1993. This research was supported by the Wisconsin Endangered Resources Cahill Gift Fund, the U.S. Fish and Wildlife Service, and the Max McGraw Wildlife Foundation.

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FACTORS AFFECTING FOOD PROVISIONING OF NESTLING BLACK-THROATED BLUE WARBLERS

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ABSTRACT.—Using video cameras at nests, we measured rates, quantities, and types of food delivered by male and female Black-throated Blue Warblers (*Dendroica caerulescens*) to nestlings of different ages and at different times of day and nesting season. Based on 89 1.5–2 h observation periods at 18 nests, all of which contained four young, we found that larval Lepidoptera comprised 60–87% of the estimated prey biomass brought to nestlings and that the female and male parents delivered approximately equal amounts of food over the nesting cycle. Food provisioning rates did not vary with time of day or with parental age, but did increase significantly with age of nestlings and decrease with time of season (early vs mid-summer). The lower rate and quantity of provisioning in mid-summer was reflected in significantly slower growth of nestlings in that part of the season, suggesting constraints on parental food provisioning, perhaps due to lower food availability. *Received 27 Aug. 1995, accepted 2 Feb. 1996.*

Successful production of offspring is an essential component of individual fitness (Stearns 1992), as well as being crucial to the maintenance of population levels for most, if not all, bird species (Nolan 1978, Virolainen 1984, Sherry and Holmes 1992, Holmes, et al. 1992. Robinson et al. 1995). Although predation at the nest is probably the single most important factor affecting breeding success of most passerine birds (Ricklefs 1969, Holmes et al. 1992, Martin 1992a), parental care of nestlings can also be important (Kuitunen and Suhonen 1991). Parental care, which includes nest building, incubation, food provisioning, vigilance, and brooding, is not only energy-demanding but also potentially risky to the survival of the parents and their lifetime reproductive success (Curio 1988). Quantities of food delivered can influence nestling survival as evidenced by brood reduction due to starvation in many passerine birds (Magrath 1990) and in some cases by starvation of whole broods (Rodenhouse and Holmes 1992, Sherry and Holmes 1992). Also, nestlings that are not well fed may beg more, which could result in the attraction of predators, leading to higher nest losses (Skutch 1949, Martin 1992b). The patterns of food delivery to nestlings and the factors that affect them are, therefore, important for understanding population processes. Information about which factors influence food delivery patterns is also useful for designing sampling protocols for future studies of reproductive biology of particular species.

In this study, we examined the rates and quantities of food delivered

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to nestlings by male and female Black-throated Blue Warblers (*Dendroica caerulescens*) breeding in a northern hardwoods forest in north-central New Hampshire. Specifically, we tested whether or not feeding rates and quantities of food delivered by males and females varied with nestling age, time of season, time of day, and/or parental age. We also considered the effect of parental provisioning by measuring the growth rates of young in the nests being videotaped.

STUDY SITE AND METHODS

This study was conducted in the Hubbard Brook Experimental Forest, West Thornton, New Hampshire. This forest consists of northern hardwoods, dominated by sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*), with a shrub layer of hobblebush (*Viburnum alnifolium*), saplings of sugar maple and especially beech, and striped maple (*A. pensylvanicum*). The ground stratum consists mostly of herbs, tree seedlings, mosses, and ferns (Bormann and Likens 1979, Holmes 1990).

At Hubbard Brook, Black-throated Blue Warblers nest at an average height of 0.6 m above ground, mostly in hobblebush but also in other shrub-level vegetation (Holmes 1994). We located most nests during the building or incubation stages and then checked them periodically until hatching. Nestlings were weighed with a 10-g Pesola balance on days 2, 4, and 6 (hatching = day 0), the last day they could be handled without causing premature fledging (Holmes et al. 1992). Parents at each nest were color banded, and aged as yearlings (i.e., in their first potential breeding season after hatching) or as older individuals (i.e., in their second or later breeding season), using plumage criteria (U.S. Fish and Wildlife Service 1977, Pyle et al. 1987). Identification of the sexes was unambiguous, due to strong sexual dichromatism in this species.

To record parental feeding rates and foods brought to nests we used two Sony camcorders and one Panasonic S-VHS Recorder (VCR) equipped with 8–10× telephoto lens. Cameras were set on tripods (0.5–1.5 m high) at distances of 3–5 m from the nest, depending on local topography and on density and arrangement of nearby foliage. The video cameras and tripods were covered with black plastic for rain protection and then draped with burlap for camouflage. If necessary, overhanging leaves around the nest were pulled aside and tied so as not to obscure the nest during taping. Any tapes containing evidence that the adults were disturbed were eliminated from the analyses. Taped sequences ranged from 1.5–2 h depending on battery life; data were converted to number of visits, or quantities of food delivered, per hour.

Between 12 June and 17 July 1991, we obtained 89 video samples at nests of 18 Black-throated Blue Warbler pairs. We restricted the nests used for analysis to those containing four young, the mean and modal brood size for Black-throated Blue Warblers at Hubbard Brook (Holmes et al. 1992). Each nest was attended by one male and one female, and none of the males was known to be polygynous (see Holmes et al. 1992, 1996). Visits to nests were video-taped when nestlings were 2, 4, 6, and 8 days of age (hatch = day 0). In this species, nestlings typically fledge late on day 8 or on day 9 (Holmes 1994). Samples were obtained from the same nests on different days, but no nests were sampled more than once per time-of-day/age-of-nestling category. Data from each recording session were categorized according to age of nestlings (see above), time of the season ("early" nests fledged young before 1 July, "late" nests after 1 July, see Holmes et al. 1992 for nesting chronology), the time of day when the nests were vidcotaped (grouped in three time intervals [EDT]: morn-

ing, 06:30–09:45 h, midday, 10:30–13:30, and afternoon, 14:00–17:00), and the age of parents (yearling vs older, see above).

From each taped sample, we recorded the number of visits made by each parent and, where possible, the number, size, and life-form (larval or adult, the latter including Arachnida) delivered to the young. Prey size was determined by comparing the length of prey item (or the prey load when there was more than one item that could not be distinguished) with the 7 mm-long exposed portion of the Black-throated Blue Warbler bill. These data were grouped into four size classes (<7 mm, 7–14 mm, 14–21 mm, >21 mm), regardless of taxa. They were then converted to biomass, based on length-mass regressions for midpoints of each size class. Conversion factors for the four size classes were 1, 2, 8, and 20 mg, respectively, following the rationale and protocol of Omland and Sherry (1994: Table 1). Estimates of food biomass delivered to the nest per hour were then obtained by summing the estimated prey biomass on each trip during the sample period, and expressing these as mg of food delivered $\cdot$brood$^{-1}\cdot$h^{-1}.

Data for both the number of feeding trips per hour and the food biomass delivered per hour were normalized by square root transformation. The relationships between food provisioning and each variable for both females and males were evaluated by analyses of variance (ANOVA). Differences between the sexes and parental age classes, where appropriate, were examined with *t*-tests. Potential differences in nestling growth in early versus late season nests was assessed by comparing (1) the mean body mass of nestlings on day 6 (mean mass per nestling in nests with 4 young, N = number of nests) and (2) the rate of gain in body mass between day 2 and day 6 (mean mass per nest on day 6 minus that on day 2, N = number of nests).

RESULTS AND DISCUSSION

The number of feeding trips and the biomass of food delivered to broods per hour by adult Black-throated Blue Warblers varied significantly with nestling age (except for feeding trips by females) and with time of season (for both sexes), but not with time of day (Table 1) or with parental age (see below). Two and three-way interactions among these variables were not statistically significant (P values > 0.2). Removal of time of day from the ANOVAS did not alter these results. As mentioned previously, brood size was not a factor in these analyses, because only nests containing four young were considered.

Effects of nestling age.—The most important factor affecting both the number of food delivery trips and amount of food delivered per nestling was nestling age. Both sexes increased their feeding visitation rates from day 2 through day 8 of the nestling phase (Fig. 1A). This trend was not statistically significant for females (Table 1), probably because they were already feeding nestlings relatively frequently on day 2 and did not increase their rate substantially between days 4 and 6. In contrast, males progressively increased their feeding visits as the nestlings became older (Fig. 1A). This difference between the sexes was also evident in comparisons of food visitation rates on particular days: on average, females made significantly more trips to the nest than did males on days 2 and 4 ($t = 4.01$, df = 38, $P = 0.000$, and $t = 3.26$, df = 46, $P = 0.002$,

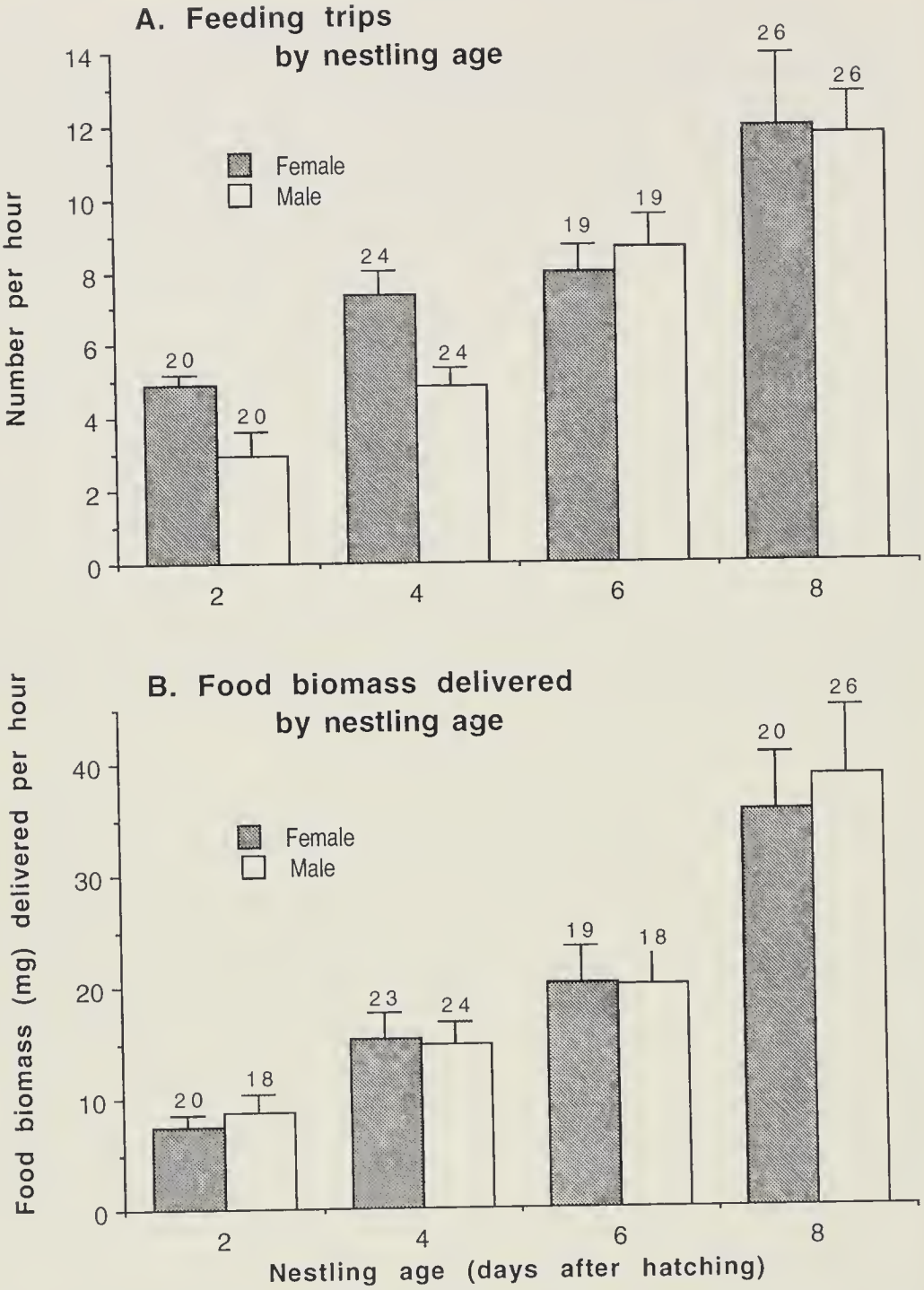

FIG. 1 Feeding rate (A) and estimated food biomass delivered (B) by female and male Black-throated Blue Warblers to broods of four young on days 2, 4, 6, and 8 following hatching (Means ± SE, N = number of 1.5–2 h video-taped samples).

TABLE 1

RESULTS OF ANALYSES OF VARIANCE (ANOVA) TESTS OF FOOD PROVISIONING BY MALE AND FEMALE BLACK-THROATED BLUE WARBLERS AT NESTS WITH FOUR YOUNG[a]

	Females				Males			
	SS[b]	df	*F*	*P*	SS[b]	df	*F*	*P*
Number of food deliveries								
Model[c]	12.50	6	1.74	0.121	41.24	6	15.90	0.000
Age of nestlings	1.25	3	0.35	0.790	38.76	3	29.89	0.000
Time of day	0.95	2	0.40	0.673	0.01	2	0.01	0.988
Time of season	5.18	1	4.34	0.040	2.13	1	4.92	0.029
Residual	110.42	88			76.69	88		
Food biomass delivered								
Model	120.47	6	11.06	0.000	119.47	6	6.93	0.000
Age of nestlings	50.71	3	9.31	0.000	53.15	3	6.16	0.001
Time of day	4.65	2	1.28	0.284	0.69	2	0.12	0.887
Time of season	9.84	1	5.42	0.023	14.24	1	4.95	0.029
Residual	256.62	81			346.52	85		

[a] Analyses were performed separately on the number of food delivery trips·h^{-1} and on the estimated food biomass (mg) delivered·h^{-1}.

[b] Sum of squares.

[c] Explained variance for full models: female number, $r^2 = 0.11$; female biomass, $r^2 = 0.47$, male number, $r^2 = 0.54$; male biomass $r^2 = 0.34$.

respectively), but not on days 6 and 8 ($t = -0.61$, df = 36, $P = 0.546$, and $t = 0.08$, df = 50, $P = 0.938$, respectively).

The quantity of food delivered to the brood increased significantly with nestling age for both sexes (Table 1, Fig. 1B). There were no significant differences between the sexes, however, in the quantity of food delivered per hour at any of the four nestling ages days sampled (*t* tests, *P* values > 0.49). Because males made fewer trips to nests on days 2 and 4 but were contributing about equal biomass (Fig. 1B), they must have been bringing larger and/or more prey per trip (see below).

The positive relationship between nestling age and feeding/food biomass delivery rate was related, as expected, to the increasing energy demands of the young, either for growth or thermoregulation. This same pattern has been reported for most species where it has been studied (e.g., Morehouse and Brewer 1968, Nolan 1978, Johnson and Best 1982, Biermann and Sealy 1982, Bedard and Meunier 1983, Breitwisch et al. 1986, Haggerty 1992). The only apparent exception is the Nashville Warbler (*Vermivora ruficapilla*) in which both males and females were reported to feed nestlings at an essentially constant rate (Knapton 1984). This study, however, examined feeding rates only on days 4 to 8 of the nestling period.

Differences between male and female passerines in the provisioning of their nestlings have been noted frequently, but there appears to be no consistent pattern. In Prairie Warblers (*D. discolor*) and Eastern Phoebes (*Sayornis phoebe*), both sexes fed about equally throughout the nestling period (Nolan 1978 and Conrad and Robertson 1993, respectively). In Yellow Warblers (*D. petechia*), males brought more food to the nest than did females when nestlings were two days old, but by day 8, males and females were delivering food at equal rates (Biermann and Sealy 1982). Female and male Savannah Sparrows (*Passerculus sandwichensis*) made approximately equal number of trips to the nest through the entire nestling period, although this varied some with brood size (Bedard and Meunier 1983). In the latter study, however, when food biomass was considered, males and females brought different quantities of food at different parts of the nestling cycle. Similarly, when food biomass estimates were made for Black-throated Blue Warblers in this study, we found that although the sexes fed at different rates at different parts of the nesting cycle, they delivered approximately equal quantities of food over the nestling period.

Effects of time of season.—Black-throated Blue Warblers made significantly fewer feeding visits and delivered less food biomass per nest per hour in mid-summer (July) than earlier in the season in June (Table 1, Fig. 2). These lowered provisioning rates in the later part of the breeding season were evident for both female and male parents. Furthermore, there were no significant differences between the sexes in their rates of feeding visits or in the quantities of food biomass delivered on any of the four sample days in either the early or the late parts of the season (t tests, P values > 0.13). The lower provisioning at nests in mid summer, therefore, was not due to one sex being a poorer provider at that time.

Other studies have found either no change in food provisioning rates during the course of a breeding season (Johnson and Best 1982), or if changes did occur, they were compensated for by an increase in the quantities of prey brought to the nest (Royama 1966). The fewer trips to the nest/hour and lower food biomass delivered by Black-throated Blue Warblers in this study could be due to several factors. First, nestlings in mid-summer may have lower energy requirements because of lower thermoregulatory costs in the warmer temperatures, although this seems unlikely in these relatively cool northern forests. Second, because the nests in mid-

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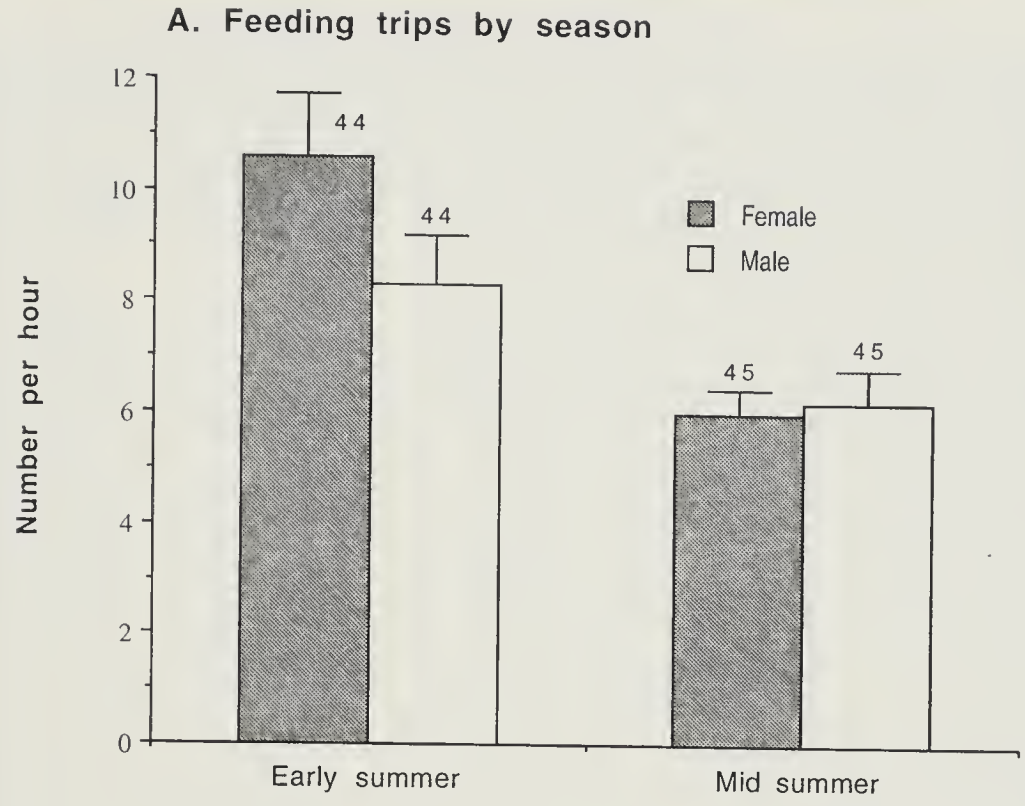
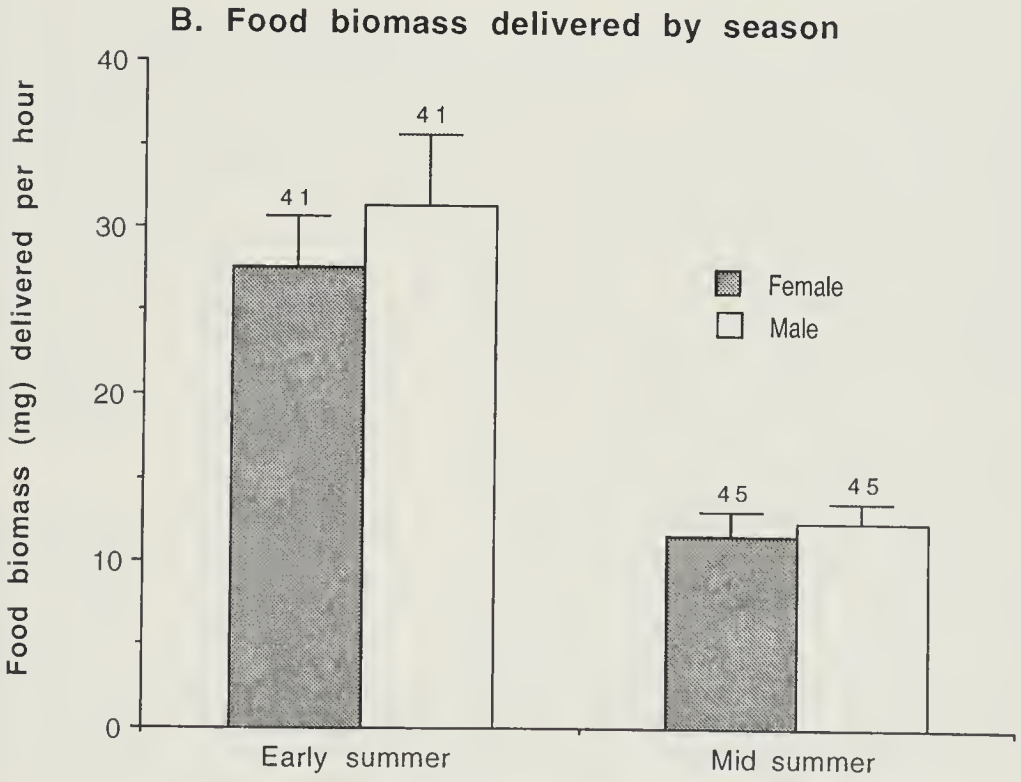
FIG. 2. Feeding rate (A) and estimated food biomass delivered (B) by female and male Black-throated Blue Warblers to broods of four young in June and July (Means ± SE, N = number of 1.5–2 h video-taped samples).


A. Feeding trips by season
Number per hour
12
10
8
6
4
2
0
44
44
45
45
Female
Male
Early summer
Mid summer


B. Food biomass delivered by season
Food biomass (mg) delivered per hour
40
30
20
10
0
41
41
45
45
Female
Male
Early summer
Mid summer

summer were either replacements for ones lost earlier in the season or were second broods (Holmes unpubl. data), perhaps they may be more "expendable" if other energy demands for the parents become more important, e.g., the onset of the annual molt or fat deposition for migration. Molt in this species, however, does not begin until early August and departure on migration doesn't occur until later in the season (Holmes 1994), so this explanation seems unlikely.

A third possible explanation for lower food provisioning of nestlings in mid-summer is that parents had more difficulty in finding food at that time of the season. If so, the reduced level of provisioning should result in slower nestling growth. To test this, we compared growth rates of nestlings in early and late season nests, as indicated by changes in body mass of nestlings between day 2 and day 6 following hatching and body mass on day 6. The mean (±SE) change in body mass of nestlings in early season nests (5.08 ± 0.16 g, N = 8 nests) was significantly higher than that for nestlings in late season nests (4.32 ± 0.21, N = 7; $t = 2.94$, df = 13, $P = 0.012$). Similarly, nestlings on day 6 in the early part of the summer were heavier (7.71 ± 0.02 g, N = 10 nests) than those in mid-summer (7.03 ± 0.30, N = 8), although these differences were only marginally significant ($t = 1.93$, df = 16, $P = 0.07$). Thus, Black-throated Blue Warbler nestlings in late season nests grew more slowly than did their early season counterparts, which could ultimately have a major impact on their post-fledging survival as has been shown by Perrins (1980) for Great Tits (*Parus major*). This finding suggests that food provisioning by Black-throated Blue Warbler parents is not always sufficient to maximize growth of their nestlings and is consistent with the proposition that food is limiting for Black-throated Blue Warblers, at least in some years or seasons (Holmes et al. 1991, Rodenhouse and Holmes 1992).

Effects of time of day.—Food provisioning by Black-throated Blue Warblers did not differ significantly with time of day, either for feeding visitation rate or food biomass delivered (Table 1). Also, there were no significant differences between the sexes in either feeding visits or food delivered at different times of day (t tests, P values > 0.22).

Nolan (1978) found little variation in foraging rate during the day for Prairie Warblers, except for an increase in the morning shortly after dawn (06:00–07:00) and a smaller increase late in the day (19:00–20:00). Similarly, Haggerty found no significant diurnal variation in provisioning rates of Bachman's Sparrow (*Aimophila aestivalis,*). More pronounced diurnal patterns have been reported for other species, e.g., Eastern Kingbirds (*Tyrannus tyrannus,* Morehouse and Brewer 1968) and Nashville Warblers (*Vermivora ruficapilla,* Knapton 1984), in which feeding rates decrease in the middle of the day and increase again later. These are

mainly species of more open habitats in which mid-day temperatures may depress insect activity or increase physiological stress on foraging adults. In the present study, Black-throated Blue Warblers nested and foraged largely in the cool, well-shaded understory of a closed-canopy forest, where diurnal variation in summer temperature and insect abundance, especially of Lepidoptera larvae, is not pronounced (R. T. Holmes, unpubl.).

Effects of parental age.—Because of relatively small sample sizes for each parental age class within a sex and the lack of independence arising from multiple samples from individual nests, we were unable to include parental age in the ANOVAs. However, we could test for parental age effects within a restricted part of the nestling period. To do this, we compared the feeding rates of yearling and older parents, both females and males, at nests containing 4 young on day 6 of the nestling period, the time when our sample was largest. The results of one-way ANOVAs indicated no significant difference in feeding visitation rate or food biomass delivered between yearling and older females ($F_{1,17} = 0.06$, $P = 0.81$, and $F_{1,17} = 0.03$, $P = 0.881$, respectively) or between yearling and older males ($F_{1,17} = 0.09$, $P = 0.768$, and $F_{1,16} = 1.51$, $P = 0.237$). Thus, at least on day 6 of the nestling period, there was no effect of age on food provisioning of nestlings for either female or male Black-throated Blue Warblers.

There is little comparative information on food provisioning rates among parental age classes for passerines. Goossen and Sealy (1982) suggested that older Yellow Warblers (*D. petechia*), because of their greater experience, should provide better care for their nestlings than first-time breeding yearlings, but they did not provide supporting data. Studd and Robertson (1989) found no difference in provisioning rate between age classes in Yellow Warblers, nor did Omland and Sherry (1994) for male American Redstarts *Setophaga ruticilla*. Current evidence thus suggests that year-old parents do about as well as older, and presumably more experienced, adults in providing food for their nestlings.

Foods delivered.—For purposes of analysis, food brought to nestlings was divided into two broad categories recognizable in video images, namely larval arthropods (almost entirely lepidopteran caterpillars) and arthropod adults (e.g., crane flies (Tipulidae) and other Diptera, some Hymenoptera and Lepidoptera, and occasional Coleoptera and Arachnida). On a biomass basis, larval insects comprised 60 to 87% of the food brought to nestlings by both females and males (Table 2). Females delivered 43 to 50% of the food biomass to the brood over the course of the nesting cycle. There were no significant differences between the sexes in larval and adult biomass delivered per hour (*t* tests, *P* values > 0.3),

TABLE 2

ESTIMATES ($\bar{x} \pm$ SE) OF FOOD BIOMASS DELIVERED TO BLACK-THROATED BLUE WARBLER NESTLINGS ON DAYS 2, 4, 6, AND 8 FOLLOWING HATCHING

	Food biomass (mg dry weight) delivered·brood^{-1}·h^{-1} for nestling age (in days)			
	2	4	6	8
Food delivered by females				
Larval insect biomass[a]	4.9 ± 0.9	12.2 ± 1.7	14.9 ± 2.4	21.8 ± 3.9
Adult insect biomass[b]	2.5 ± 0.6	3.2 ± 0.8	5.8 ± 1.6	14.0 ± 5.0
% larvae	63%	80%	78%	60%
(N)[c]	(20)	(23)	(19)	(20)
Food delivered by males				
Larval insect biomass[a]	7.7 ± 1.7	12.5 ± 1.9	15.2 ± 2.3	27.4 ± 5.1
Adult insect biomass[b]	1.1 ± 0.5	2.2 ± 0.7	4.9 ± 1.2	11.4 ± 2.5
% larvae	87%	84%	79%	73%
(N)	(18)	(24)	(18)	(26)
% Total food biomass delivered by females	46%	50%	49%	43%

[a] Mostly Lepidoptera larvae.
[b] Flying insects, mostly Diptera, with occasional Hymenoptera and Coleoptera.
[c] Sample sizes represent number of video samples per nestling age class during which prey could be classified.

although variances were high (Table 2). There was a trend for males on day 2 to bring a greater biomass and percentage of larval prey than did females (Table 2), which compensates for their fewer trips at that stage (see below, Fig. 1A). Other studies have noted that male paruline warblers sometimes bring larger prey than do females, especially during the early part of the nestling period (see Nolan 1978, Biermann and Sealy 1982, Omland and Sherry 1994). In the present study, as a result of changing food loads (and partly by changing prey types), male and female Black-throated Blue Warblers contributed about equally in terms of prey biomass delivered to their broods over the course of their nesting cycle.

In conclusion, food provisioning rates of both male and female Black-throated Blue Warblers varied mostly with age of nestlings (especially for males) and with time of season for both parents, with males and females contributing about equally to the provisioning of their offspring. The lower rate of feeding visits and of food biomass delivered in mid-summer was correlated with a decreased rate of nestling growth in those nests compared to earlier in the season. Thus, food availability, at least in some times and places, provides a constraint on nestling growth rates which, in turn, might influence post-fledging survival. Food availability also affects the frequency of double-brooding and, as a consequence, the annual

reproductive productivity of this species (Holmes et al. 1992). It is important to acknowledge that these results derive from studies conducted in only one year and one place. Replication in other locations, and especially over more years, will be required to determine the generality of these patterns. Also, because of large variances and intercorrelations between variables, larger sample sizes would be helpful for detecting patterns. Finally, some habitats or even territories within habitats occupied by Black-throated Blue Warblers may be more productive than others, affecting prey availability, and thus influencing food capture and delivery rates of the foraging parents. Thus, food provisioning patterns correlated with measures of food availability in different habitats or on a territory-to-territory basis would help to clarify causes underlying the patterns observed in this study.

ACKNOWLEDGMENTS

We thank the 1991 field crew at Hubbard Brook, especially P. P. Marra and T. W. Sherry, for their help, advice, and encouragement throughout this project. Steve Sloan assisted with the data analysis. The project was supported in part by the Presidential Scholars Program of Dartmouth College and by an REU supplement to a research grant from the National Science Foundation to Dartmouth College. P. Marra, T. Sherry, S. Sillett, and P. Hunt provided helpful comments on the manuscript.

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Wilson Bull., 108(3), 1996, pp. 480–495

BREEDING BIOLOGY AND NATURAL HISTORY OF THE BAHAMA SWALLOW

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ABSTRACT.—The Bahama Swallow (*Tachycineta cyaneoviridis*) is an obligate secondary cavity-nester endemic to the pine forests of four islands in the northern Bahamas. The near-threatened status of this poorly known species stems from the limited extent of pine forest breeding habitat, a history of logging in that habitat, and potential competition from exotic secondary cavity-nesters. Natural nest sites of Bahama Swallows on Grand Bahama generally were abandoned woodpecker cavities and nests in all types of cavities were built from pine needles, *Casuarina* spp. twigs, and grass. Mean clutch size was 3.0 and the pure white eggs were slightly larger than those of Tree Swallows (*T. bicolor*). Both the mean incubation and nestling periods, 15.8 days and 22.7 days, respectively, were longer than those of Tree Swallows. Hatching success and nestling success were 87% and 81%, respectively, giving an overall success rate of 70%. One case of double-brooding was documented, and two other likely cases were noted. Weekly surveys of adults in pine forest habitat on Grand Bahama during breeding gave a linear density of 0.18–0.25 pairs-km^{-1}. The result from a single survey on Andros (0.21 pairs-km^{-1}) corresponds to survey results on Grand Bahama in the same period and very roughly agrees with the outcome of a 1988 survey. *Received 13 October 1995, accepted 18 February 1996.*

The Bahama Swallow (*Tachycineta cyaneoviridis*), currently listed as near-threatened (Collar et al. 1992), is a poorly known endemic of the islands of Andros, Abaco, New Providence, and Grand Bahama in the northern Bahamas (American Ornithologists' Union 1983). Like other members of the *Tachycineta* genus, the species is an obligate secondary cavity-nester (Turner and Rose 1989). Bahama Swallows nest mainly in cavities in Caribbean pine trees (*Pinus caribaea*), and their breeding season distribution corresponds to the distribution of the pine forest (Smith and Smith 1989). Smith and Smith (1989) summarized most known information about the species from previously published anecdotes and their own limited observations, yet much remains unknown. Neither its nest nor eggs has been reliably described (Smith and Smith 1989), contrary to reports otherwise (Turner and Rose 1989). The need for more information about the Bahama Swallow is obvious if we are to understand the conservation needs of this near-threatened species.

Conservation concerns for the Bahama Swallow stem from the limited extent of their pine forest habitat and a history of logging in that habitat. A recent silviculture inventory gave the total area of pine forest in the Bahamas as 2042 km^2 (Allan 1986) and, though the total extent of forest

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apparently has not changed due to logging (Henry 1974), most of it is second growth (Swenson 1986). No logging in the Bahamas has occurred since the early 1970s (Henry 1974), but history shows how quickly this limited habitat can be altered. Over 70% of the forest on Grand Bahama was harvested in just three years during the peak of logging there in the 1950s (Henry 1974). This comprised nearly 30% of all pine forest in the Bahamas. Given the limited nature of breeding habitat and the extent of loss possible through logging, concern about the conservation of the Bahama Swallow is appropriate. Conservation problems caused by loss of habitat could be exacerbated by competition for nest sites with exotic secondary cavity-nesters, House Sparrows (*Passer domesticus*) and European Starlings (*Sturnus vulgaris*), which are also present in the Bahamas.

As the first step in addressing the conservation concerns associated with the Bahama Swallow, I report here the findings of recent research on their natural history and breeding biology. I use the Tree Swallow (*T. bicolor*), a temperate congener, as the basis for comparing various aspects of Bahama Swallow breeding biology since none of the tropical congeners of the Bahama Swallow (e.g., Mangrove Swallow *T. albilinea*) is as well-known. I also describe results of surveys that expand upon a pilot survey in 1988 (Smith and Smith 1989) and which provide baseline information for monitoring the population size of the Bahama Swallow.

STUDY AREA AND METHODS

I studied breeding Bahama Swallows on Grand Bahama (26°40′N, 78°30′W) in the Bahamas from mid-March through June 1995. I found nests in natural sites throughout the forested part of the island between Freeport and McClean's Town, about 75 km east of Freeport. Most nests in artificial sites were located at an abandoned U.S. Air Force missile tracking base (hereafter "Missile Base") near Freetown (26°37′N, 78°21′W) about 35 km east of Freeport. All nests were either in or adjacent to tracts of secondary pine forest which make up most of the interior of Grand Bahama east of Freeport. Most nests in natural sites were found by observing swallows loitering on dead pine trees ("snags"). Nests at the Missile Base were found by systematic searches of artificial cavities and by observing swallows. The presence of a nest in an inaccessible nest site (i.e., most snags) was inferred by seeing swallows entering a cavity with nest material or by observing birds entering a cavity on several different occasions.

Most nests in natural sites were observed from the ground once every two or three days, but some were observed only once or twice in two weeks during the first few weeks of the breeding season. Observations generally lasted only long enough to confirm that a nest was still active. Activity was determined to have ceased at a nest when either two 0.5 h observations on consecutive days showed no activity or when a single 1 h observation revealed no activity. However, I often made extra observations to confirm lack of activity. If activity at a nest ceased without my having observed about three weeks of frequent nest visits (which I assumed to be feeding visits), the nest then was assumed to have failed unless some other clue (e.g., previous sightings of nestlings looking out of the hole) indicated probable fledg-

ing. Dates of either fledging or failure of a nest were estimated to be the midpoint between the last observation of activity at the nest and the first observation with no activity. Dates of clutch completion and hatching were estimated by subtracting the length of the average incubation and nestling periods (calculated from detailed observations of nests at the Missile Base) from the estimated fledging date.

I examined some nests in natural sites using a 1-m fiberscope, reaching the cavities with a 10-m extension ladder (Rohwer 1988). The limited resolution and depth of field of the fiberscope did not allow precise counts of chicks or eggs in a nest, so I have accurate counts of eggs or chicks only for those nests I excavated. Cavities were excavated by carefully enlarging the existing entrance hole of the cavity with a saw. Cut-away pieces from excavations were replaced and secured with wire, thus maintaining the integrity of the cavity.

Some artificial cavities used as nest sites were nest boxes (both standard and Peterson box designs) or plastic Purple Martin (*Progne subis*) gourds (Carroll Industries, Van, Texas) I erected at the Missile Base. Nests in accessible artificial cavities were observed daily prior to egg-laying, during egg-laying, and for several days prior to hatching. Eggs were measured with dial calipers to the nearest 0.1 mm and weighed to the nearest 0.1 g with an electronic balance (Pocket Pro 150-B, Acculab, Newtown, Pennsylvania), generally on the day of laying.

At nests in accessible artificial cavities, I took measurements of chicks younger than 18 days old nearly every day. Mass was measured with the balance to the nearest 0.1 g. Straightened, flattened wing chord of the right wing was taken with dial calipers to the nearest 0.1 mm until the chord was about 15 mm long and thereafter with a ruler to the nearest 0.5 mm. Chicks within the same nest were identified by uniquely marking their wings or legs with a permanent felt-tip marker. These markings were superseded by color bands and numbered aluminum bands when the chicks were 7–14 days old. To avoid premature fledging, most chicks older than 17 days were simply counted without handling. Thus nestling periods are reported on a nest-wise basis (i.e., the period between the first chick hatching and the last chick fledging) instead of for individual chicks. Three late-season nests at the Missile Base received only enough visits to determine the number of chicks hatching and fledging. Permission to salvage and export several nests, eggs, and chicks was granted by the Bahamas Dept. of Agriculture.

Censusing or surveying highly mobile birds is difficult and my attempts to apply distance sampling techniques (Buckland et al. 1993) to survey Bahama Swallows along forest roads on Grand Bahama were unsuccessful. The distance data required for that method was impossible to collect, since swallows were often sighted while flying without any reference object nearby to which distance could be measured or even roughly estimated. Ultimately, I simply counted all swallows, whether foraging or perched, along separate survey routes in three areas of Grand Bahama on different days. Since I rarely observed other swallows on Grand Bahama during the breeding season, I assumed that all swallows I could not identify were Bahama Swallows. The three routes generally were covered on consecutive days. Weather on survey days typically was sunny and warm, with the few exceptions being slight overcast or cloudy conditions. The Eastern Lucaya route was 19 km of sparsely settled, relatively undeveloped subdivisions covered mostly with secondary forest and a dense network of roads. The second route covered 45 km in the Lucayan Estates subdivision, an area of secondary forest without any housing but with several farms and a dense road network. The East End route was 58 km long and used a logging road which ran down the center of much of the island. The eastern two-thirds of that route was relatively undisturbed secondary forest, and the remainder went through parts of Lucayan Estates. The routes were driven at a speed of 10–14 kph using either a moped (in May) or automobile (in June), beginning between 06:30 and 07:00 EST. I was both driver and observer for all Grand Bahama surveys.

In an earlier survey of Andros, Smith and Smith (1989) drove 96.4 km through the pine forest of that island at speeds under 30 kph on two days, 20–21 May 1988. An assistant and I performed one survey on Andros covering 76.0 km of the 1988 route (P. Smith, pers. comm.) following the 1988 protocol for the single day of our survey, 26 May 1995. For purposes of estimating the number of breeding pairs in all surveys, I assumed that groups of either one or two swallows represented one breeding pair and that groups of either three or four birds represented two breeding pairs. Juveniles identified as such were not counted.

RESULTS AND DISCUSSION

Nesting activity.—On 31 March, I noted the first exhibition of nesting behavior by Bahama Swallows since I had begun observations in mid-March. Swallows repeatedly flew up to and hovered in front of louvered access panels on the upper floors of a 12-story building near Freeport. I interpreted this activity as prospecting for nest sites and saw similar behavior at the same building on 2 April, when swallows approached the undersides of balconies and eaves. The first nesting behavior I observed at a natural nest site was on 2 April when two to four swallows flew around and approached a woodpecker hole in a snag. I observed a swallow taking nest material into that hole on 10 April. At this and other nests in natural sites, swallows were active at their nests only between about 07:00 and 11:00 during the nest-building stage, and attempts to find nests by observing adults at natural sites were fruitless later in the day.

Overall, I found 18 nests in natural nest sites: 10 nests seemed to be successful, five failed without fledging young, and three nests were still active when I left the island. To establish that nests in natural and artificial cavities did not differ in obvious ways, I examined nine of the 18 natural nests with a fiberscope. I found chicks in five of them, eggs in three of them, and neither eggs nor chicks in the last. In four nest sites that I excavated, I found incubated clutches of three eggs in each of two cavities, three chicks in another, and a partial nest in the last. What I saw of nests in natural cavities convinced me that they were similar to nests in artificial cavities with respect to clutch size and types of nest material used. I assume that most other aspects of breeding biology do not differ greatly between swallows nesting in natural and artificial sites.

Nest-site characteristics.—Although Bahama Swallows do use cavities in live trees (Smith and Smith 1989), all 18 nests I found in natural nest sites were in pine snags. All of those sites were abandoned woodpecker holes, except one which was in a large, cracked branch. The pine snags used for nesting had a mean diameter at breast height of 22.3 cm (N = 18, SD = 4.26, range: 17.0–28.3 cm). The mean height of the snags was 9.6 m (N = 18, SD = 2.17, range: 6.7–12.8 m), while the mean height of the cavities was 8.8 m (N = 18, SD = 1.94, range: 6.0–11.4 m). The

closest active nests that I found in natural cavities were about 150 m from each other.

All but two of 14 nests I found in artificial cavities were at the Missile Base. Types of artificial cavities used for nesting included housings of street lights (2 nests), a horizontal pipe (ca 5–6 cm diameter) (1 nest), a gap (less than 10 cm) between two sections of wall in the side of a building (1 nest), an electrical conduit box with the only access being a 42 mm diameter hole in the 15 cm × 13 cm floor of the box (1 nest), a Peterson-style nest box with a 38 mm diameter hole (1 nest), a standard nest box with a 38 mm diameter hole and 14 cm square floor (1 nest), an artificial nest gourd with a 55 mm diameter hole (1 nest), and rooftop ventilation units with rectangular access holes 95 mm wide by 28 mm high (6 nests in 5 units). The height of these artificial cavities ranged from 3.0 m for the Peterson box attached to a utility pole to 13.2 m for the pipe nest. The nest between two wall sections was an exception since it was at the top of the 12-story building at which I first saw nesting behavior. The two closest active nests were in ventilation units 8.8 m apart on top of the same roof.

Nest construction.—During observations of nest building at natural and artificial nest sites, I never saw both birds of a pair carrying nest material. I assumed that just one bird of each pair, which I took to be the female, did most, if not all, of the nest construction. The male often escorted the female while she was gathering nest material. I observed birds gathering nest material from the edges of paved and unpaved roads as well as from the middle of grassy areas that were recently mown. Caribbean pine needles, grass, and *Casuarina* spp. "needles" (actually fine, segmented twigs of this exotic tree) formed the bulk of the nests I examined in both artificial and natural nest sites. I observed one bird travel over 200 m from its nest site to collect material, but most trips for nest material by other birds were less than 100 m.

The period from when nest building began until clutches were initiated was 14–18 days in four nests built from scratch in artificial cavities. This period might be shorter for nests in natural sites since they contained less nest material than those in artificial sites. The masses of material from two nests collected from pine snags were quite small (9.0 g and 17.1 g) compared to the masses of material from four nests in artificial sites built completely in the season of the study (18.0 g, 41.6 g, 48.2 g, and 114.9 g). This difference may result from the generally larger volume of the artificial cavities. I collected eight nests, two from snags and six from artificial sites, after fledging or abandonment of the nests and deposited them with the Vertebrate Collection at Cornell Univ., Ithaca, New York.

Nest lining materials.—Nests were lined with a variety of materials,

both naturally occurring and artificial. Flakes of pine bark were common in nests, and I saw swallows pulling bark directly off trees on several occasions. Though not every nest contained bark, most contained 1–5 pieces of about 1–3 cm^2. Small downy feathers, seemingly originating from other passerines, were the other common natural lining material. Nests usually contained 1–5 such feathers, markedly fewer than the scores of waterfowl feathers often found in Tree Swallow nests (P. Allen, pers. obs.; Winkler 1993). The largest number of feathers I found in a nest was 15–25 flamingo feathers in a nest in a pine snag on the grounds of the Rand Nature Centre which maintained a small, captive flock of Greater Flamingos (*Phoenicopterus ruber*).

Other natural lining materials I found in nests included small dry leaves, pieces of skin shed from small lizards, yellow flower petals (found in only one nest), and a pale yellow butterfly wing (found in only one nest). In one incomplete nest in a snag less than 500 m from the seashore, I found several dried strands of turtle grass (*Thalassia testudinum*), a sea grass which commonly washes up on beaches. This may explain an observation of Bahama Swallows gathering mouthfuls of "seaweed" and flying towards the forest (Todd and Worthington 1911).

Artificial material in nest linings was most abundant at the Missile Base where litter was plentiful. Bits of shredded plastic wrap, small pieces of newspaper, facial tissue, and regular paper were common in nests there. These materials were presumably used because of their gross similarity to feathers. A few nests at the Missile Base also contained paint chips from paint peeling off buildings. If the birds actually pulled the paint chips off the buildings instead of picking them off the ground, then the actions required to do this would be similar to those used for collecting pine bark.

Eggs.—The eggs I examined from two nests in snags and 10 nests in artificial cavities were larger, on average, than Tree Swallow eggs in length, width, and mass (Table 1; masses of eggs from the two snags excluded because the eggs were not freshly laid). The mean clutch size was 3.0 eggs in these 12 nests and in an additional nest in an artificial cavity (Table 1). This is the same clutch size reported for a Caribbean congener, the Golden Swallow (*T. euchrysea*) (Turner and Rose 1989) but, not surprisingly, it is much smaller than for Tree Swallows (Table 1). Of these 11 nests in artificial cavities, two had clutches of two eggs, seven had three-egg clutches, and two had four-egg clutches. The two nests in natural cavities both had three-egg clutches. As with Tree Swallows (P. Allen, pers. obs.; Robertson et al. 1992), the color of freshly laid eggs was white, but translucent and slightly pinkish, changing to pure white after a few days of incubation. In all nests where laying was ob-

TABLE 1

COMPARISON OF BAHAMA SWALLOWS AND TREE SWALLOWS FOR SEVERAL ASPECTS OF BREEDING BIOLOGY

	Bahama Swallow			Tree Swallow			
	N	$\bar{x} \pm$ SD	Range	N	$\bar{x} \pm$ SD	Range	P[d]
Egg length (mm)[a]	36	19.4 ± 0.72	17.2–20.6	2295	19.0 ± 0.90	16.0–22.8	*
Egg width (mm)[a]	36	13.9 ± 0.40	12.9–14.6	2292	13.6 ± 0.47	11.9–15.4	***
Egg mass (g)[a]	30	2.0 ± 0.19	1.6–2.3	835	1.8 ± 0.17	1.4–2.5	***
Clutch size (eggs)[a]	13	3.0 ± 0.58	2–4	847	5.4 ± 0.91	3–8	***
Incubation period (d)[a]	5	15.8 ± 1.10	15–17	235	14.5 ± 1.13	12–19	*
Hatching success[b]	30	86.7%	33.3–100	10,107	86.9%	—	—
Nestling success[b]	26	80.8%	0–100	21,130	83.1%	—	—
Nestling period (d)[a,c]	6	22.8 ± 1.21	22–25	554	20.6 ± 1.63	16–29	**

[a] Tree Swallows in upstate New York (D. Winkler, unpubl. data).
[b] Tree Swallows from several studies (Robertson et al. 1992).
[c] Calculated for Tree Swallows on a nest-wise basis, just as with the Bahama Swallows.
[d] Results from *t*-tests comparing means using equal or unequal variances as appropriate. * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$.

served, eggs were laid one per day in the morning. I never observed Bahama Swallows copulating during this study.

Incubation.—Observations of five nests in artificial cavities yielded no consistent indication as to when incubation began. Even after the clutches were complete and incubation had presumably begun, eggs were often unattended when I checked the nests. This pattern may have resulted from often visiting nests in the early afternoon, generally the hottest part of the day. However, defining the incubation period as starting on the day the last egg was laid and ending on the day the first egg in the nest hatched, three nests had incubation periods of 15 days, and two nests had incubation periods of 17 days, giving a mean of 15.8 days (Table 1). This is over one day longer than the incubation period for Tree Swallows in upstate New York (Table 1). Though I did not often capture birds on the nest, there was no indication that males shared incubation responsibilities.

Hatching and survival.—Of the seven nests I visited daily during hatching, the eggs in three nests, two with two-egg clutches and one with a three-egg clutch, hatched in the same 24-hour period. The eggs in the four remaining nests, each containing three or four fertile eggs, hatched

over a period of 48 h. In those seven nests and in three late-season nests, 26 chicks (87%) hatched from 30 eggs (two eggs in one nest and one egg in a second nest were infertile; an additional egg was missing). Of the 26 chicks that hatched, 21 (81%) eventually fledged, giving an overall egg-to-fledgling success rate of 70%. The hatching and nestling success rates of these Bahama Swallows correspond closely with those of Tree Swallows from several studies (Table 1). The success rates for both these species are for birds nesting in artificial cavities, and success may be lower in natural cavities.

One three-day-old chick was found dead of unknown causes in its nest, while its nest mates remained in good health. One entire brood of three chicks was lost because they fell out of the ventilation unit that housed their nest. One other chick apparently was killed when the motor was activated in the ventilation unit that housed its nest. I salvaged three of these chicks and one of the infertile eggs, depositing them at Cornell. These are the only such specimens known for the Bahama Swallow (Smith and Smith 1989).

Nestling period and fledging.—In six successful nests that I monitored closely, the fledging period was 22 days for four nests, 23 days for the fifth nest, and 25 days for the remaining nest, giving a mean of 22.7 days (Table 1). This nestling period is two full days longer than that of Tree Swallows in upstate New York (Table 1). The siblings from three nests each containing two chicks fledged in the same 24-hour period. Siblings from another nest containing three chicks fledged over a 48-hour period. In two other nests with broods of three young, the fledging period was unknown because of imprecise counts of the young.

Chick development.—The rate of mass gain for Bahama Swallow chicks from seven nests was slower than that of Tree Swallows (Fig. 1), but the period during which chicks rapidly increased mass (days 1–12) was similar to that for Tree Swallow chicks. The mass of chicks from both species plateaus near their adult mass at about day 13 (Fig. 1). Growth rates, calculated by fitting a logistic curve to daily means of mass, show that Bahama Swallows ($K = 0.363$) grow more slowly than Tree Swallows ($K = 0.396$) using Tree Swallow data from McCarty (1995). Adult wing lengths of Bahama Swallows are about 4 mm shorter than those of Tree Swallows (Turner and Rose 1989), and the average length of Bahama Swallow wing chords was 2.3 mm shorter than, those of Tree Swallows for days 10–19 (Fig. 2).

In most respects, newly hatched Bahama Swallow chicks were similar to newly hatched Tree Swallow chicks (P. Allen, pers. obs.). The one exception was that all Bahama Swallow chicks were hatched with several down feathers (neossoptiles) already formed. Tree Swallows in New York

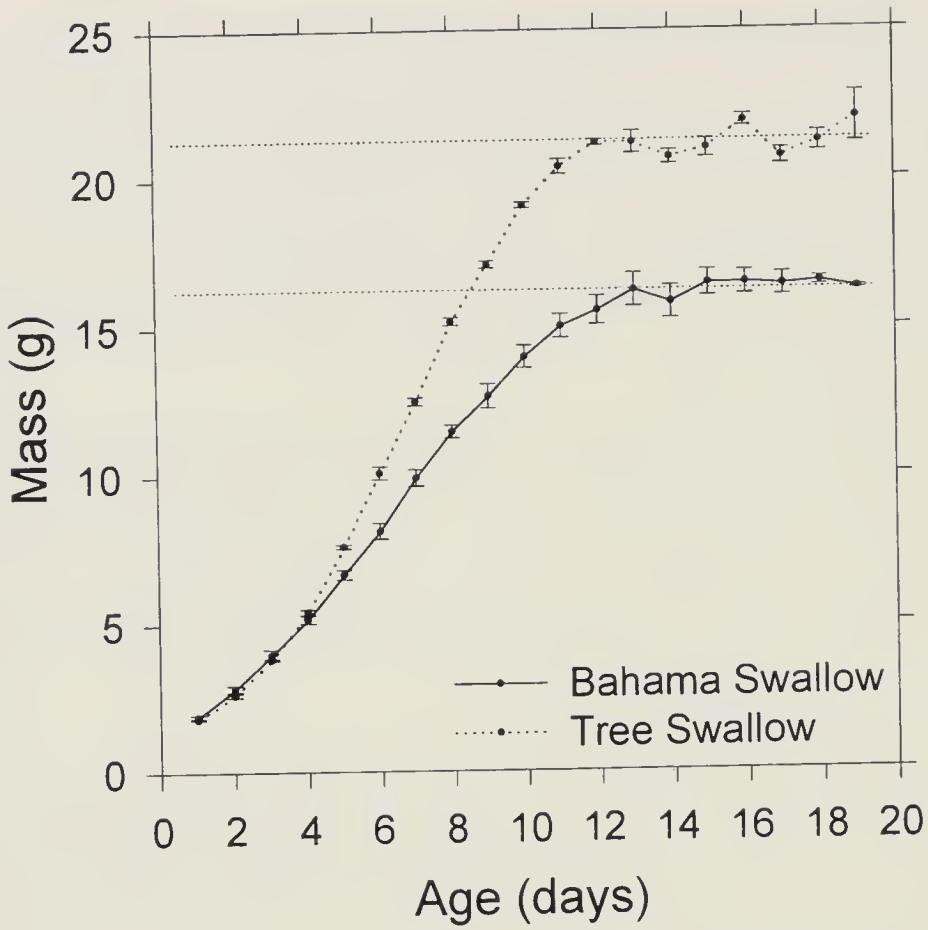

FIG. 1. Mass (means ± 1 SE) of Tree Swallow (McCarty 1995) and Bahama Swallow chicks. Upper, dotted horizontal line shows adult mass of 21.3 g for Tree Swallows from McCarty (1995). Lower, dotted horizontal line shows mean mass of four breeding Bahama Swallow females captured at the Missile Base (16.3 g). This value corresponds with low end of mass range (16.3–19.5 g, mean 17.5 g) from museum specimens (Turner and Rose 1989).

often hatch completed naked and only occasionally hatch with one or more wispy down feathers (P. Allen. pers. obs.). In Bahama Swallows, dark feather tracts began showing underneath the skin on the wings by the second day. On the third day, tracts were visible on the head and back as well. Hair-like shafts of primaries as well as back and chest feathers began breaking through the skin on the fourth and fifth days. By the seventh day, the shafts of body feathers were less than 1 mm long. Primary and tail feathers began emerging from their shafts on about day nine or ten. By day ten, body feathers were emerged 1–2 mm from their shafts. The eyes of Bahama Swallow chicks began to open on their fifth day. Chicks' eyes were just small slits on days five or six with the slits widening until being fully rounded by the tenth day.

Parental care.—At least two adults, which I took to be the parents,

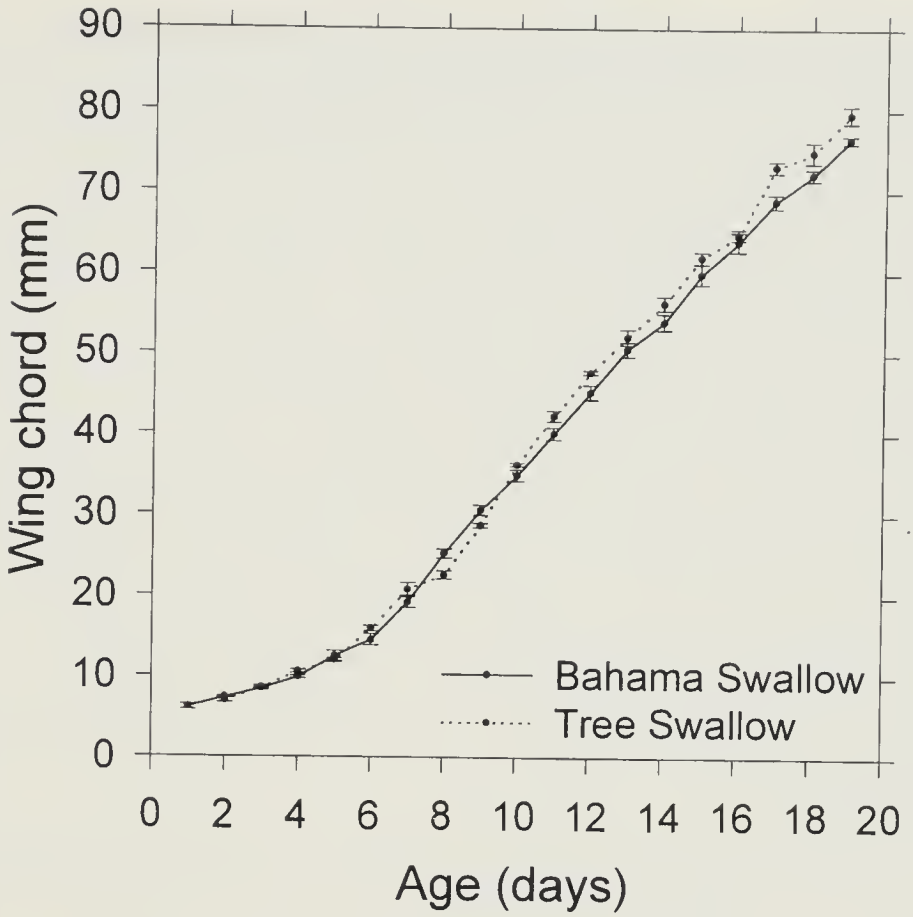

FIG. 2. Straightened, flattened wing chord (means ± 1 SE) of Tree Swallow (McCarty 1995) and Bahama Swallow chicks.

fed young at most nests. At the Missile Base adults from neighboring nests assisted in defending nests against me during daily visits. In contrast to Tree Swallow nests, where it is common to find the entire nest well-covered in fecal matter after fledging (P. Allen, pers. obs.; Robertson et al. 1992), most Bahama Swallow nests in artificial cavities were clear of fecal material after chicks fledged. Either Bahama Swallow parents provided nest sanitation throughout the nestling phase or chicks were able to defecate out of the entrances to their cavities. However, I did not note much fouling of the area immediately below nests which would have indicated that the nestlings were responsible for sanitation.

Fledglings.—Observations of post-fledging chicks were difficult to obtain. In one case, I observed four fledglings (identified by their yellow gapes) perched in a tree with an adult feeding them. In another instance, I found four color-marked sibling fledglings in a group less than 500 m from their nest six days after the last chick had fledged from their nest.

Double broods.—Of the 12 nests at the Missile Base, at least one, and

possibly three, represented second broods after the successful fledging of a previous brood. I verified double brooding by a female banded at her first nest on 17 May while feeding chicks. She was captured again on 21 June on a second nest in a ventilation unit 10.7 m away from the first nest on the same rooftop. The first brood had fledged on 29 May and the second clutch was initiated on 18 June in a nest that I had found in April and identified as being an unused nest from a previous season. Some new nest material had been added to that nest, and rusty flakes of metal had been removed from the nest bowl prior to egg-laying. Four chicks fledged from the first brood, and two chicks fledged from the second.

Another possible double-brood attempt was a clutch of three eggs I found on 16 June in the same nest from which three chicks had fledged on 4 June. The second brood in that nest produced two fledglings. Another possible case of double-brooding was a clutch initiated on 14 June in a nest box within 25 m of an inaccessible nest that was active until sometime during the first week of June. The initiation of this late clutch falls within days of the initiations for the two other double-brood nests, after a period of more than four weeks without a known clutch initiation at the Missile Base.

I made a special effort to look for renewed nesting activity at natural sites in mid-June but was unable to confirm any other possible second-brood nests. Finding such nests might be especially difficult if nests used earlier in the season were simply reused without more nest building. The last search for new nests at the Missile Base was on 26 June, so I do not know if there were more late-season nests initiated there after that date.

Overall phenology.—The mean date of clutch completion for nine nests in snags and eight nests in artificial cavities (which excludes the three late-season nests) was 5 May (SD 6.96, range: 20 April–15 May). The average date of hatching for those clutches was 20 May (SD 6.98, range: 5 May–28 May), and the mean fledging date was 11 June (N = 16, SD 7.30, range: 27 May–22 June). For the two late-season nests in which I observed egg-laying, the average date of clutch completion was 18 June. The mean estimated dates of hatching and fledging for those two broods were 4 July and 26 July, respectively.

Interspecific competition.—Bahama Swallows nesting in natural nest sites had numerous interspecific agonistic interactions with four other cavity-nesting bird species. Two were native species, the Hairy Woodpecker (*Picoides villosus*) and La Sagra's Flycatcher (*Myiarchus sagrae*). The other two, House Sparrow (*Passer domesticus*) and European Starling (*Sturnus vulgaris*), were exotic. In two interactions with woodpeckers, swallows harassed woodpeckers which were in possession of nest sites, but in both cases the woodpeckers remained in control of the cavities.

However, I did find two cases of swallows nesting quite close to woodpeckers. In one instance, active swallow and woodpecker nests were 30 m apart, and in another, the nests were 75–100 m apart. I observed a swallow being displaced from the rim of a nest-hole in a snag by a flycatcher bringing either food or nest material into the cavity. In two other cases, flycatchers perching at former swallow nest sites were displaced by swallows, even though the swallow chicks had already fledged. I found one instance of flycatchers and swallows nesting within 100 m of each other. In a case that is difficult to interpret, I excavated a nest site several weeks after I had seen swallows entering the cavity, and found it filled with typical House Sparrow nest material but with four rotten flycatcher eggs at the bottom. I observed no direct interactions between House Sparrows and Bahama Swallows. However, one cavity in which swallows were nest building was later usurped by sparrows which successfully raised a brood of young there. In another instance, I found a pair of sparrows inspecting a cavity in which there had been an active swallow nest with eggs about two weeks earlier. However, I do not have observations for the intervening period to give any hints as to whether the swallows had abandoned because of the sparrows. The Missile Base had a healthy population of breeding House Sparrows which seemed to exclude swallows from nesting in sites they might typically choose in the absence of sparrows. The sparrows had a monopoly on nest sites under the eaves of the roofs, while the swallows nested, for the most part, in sites that gave no means of clinging to the entrance hole or perching before entering the cavity. Such sites were probably difficult or impossible for sparrows to access. I observed very few interactions between starlings and swallows, but I did find one active starling nest within 75 m of a swallow nest.

Although the exotic cavity nesters have the potential to impact greatly the Bahama Swallow through competition for nest sites, I found these species mainly within about one kilometer of human structures or other disturbance. I never observed either species in undisturbed secondary forest, but House Sparrows were at farms in the middle of the secondary forest. As human development and disturbance encroach on the forest, it is inevitable that the local ranges of these exotics will spread.

Previous surveys and density estimates.—Emlen (1977) estimated a Bahama Swallow density of 11.0 birds-km^{-2} in pine forest during the breeding season by surveying a total of 21.5 km of transects using the coefficient of detectability methodology (Emlen 1971). Using Henry's (1974) estimate of the total pineland area extant at that time (1782 km^2), Emlen's density figure results in a population estimate of just under 20,000 birds in the entire species' breeding range. Caution should be used

before considering this quick extrapolation as a true reflection of the Bahama Swallow population during that study, since the survey transects seemed to have been restricted to prime breeding habitat (Emlen 1977). Also, Emlen (1977) was mainly concerned with making relative, interspecific comparisons among species and did not attempt to make absolute estimates of population sizes.

Smith and Smith (1989) is the only other source of quantitative data for the Bahama Swallow. From a simple road survey in 1988, they estimated the density of breeding Bahama Swallows at 2.6 birds-km^{-2} (Smith and Smith 1989). Using this density estimate and Henry's (1974) estimate of pine forest area, the total breeding population of the Bahama Swallow would have been about 4800 birds. Smith and Smith (1989) conceded the imprecision of the estimate but felt the result was of the correct magnitude, between 1000 and 10,000 living Bahama Swallows. This estimate is quite different from one derived from Emlen's data, but it is debatable whether the difference in the two results reflects an actual decrease in the Bahama Swallow population, at least of the magnitude indicated. A direct comparison between the two results can be misleading, since the methods used were different.

Grand Bahama surveys.—In the surveys I performed, the results from each of the three individual routes were somewhat irregular (Fig. 3; Eastern Lucaya range: 0.10–0.56 pairs-km^{-1}; Lucayan Estates range: 0.11–0.30 pairs-km^{-1}; East End range: 0.12–0.27 pairs-km^{-1}). A weighted average of the sightings from the three routes showed a pattern of increasing frequency of sightings, from 0.17 pairs-km^{-1} to 0.25 pairs-km^{-1}, during the period between the average dates of hatching and fledging (Fig. 4). This is consistent with adult swallows spending more time foraging in response to an increased demand for food as their chicks develop. Estimating breeding density from these results would be misleading because of the assumptions required to do so (e.g., that only birds breeding within a certain distance of the road were sighted) and because of bias introduced by what seemed to be an affinity to the road by the birds. Instead, the survey results should be considered indices to the population size.

Andros survey.—The 1995 Andros survey served to make a direct comparison between contemporary survey results and those of Smith and Smith (1989) without complications in interpretation arising from different protocols or routes. In 1988, Smith and Smith (1989) observed 0.28 pairs-km^{-1}. In 1995, we saw eight single swallows and eight two-somes while covering just 70% of the 1988 route, giving a sighting rate of 0.21 pairs-km^{-1}. Though the 1995 result represents a 25% decrease from the 1988 survey, the limited nature of the Andros surveys precludes the conclusion that the decrease reflects a population decline. However, since the

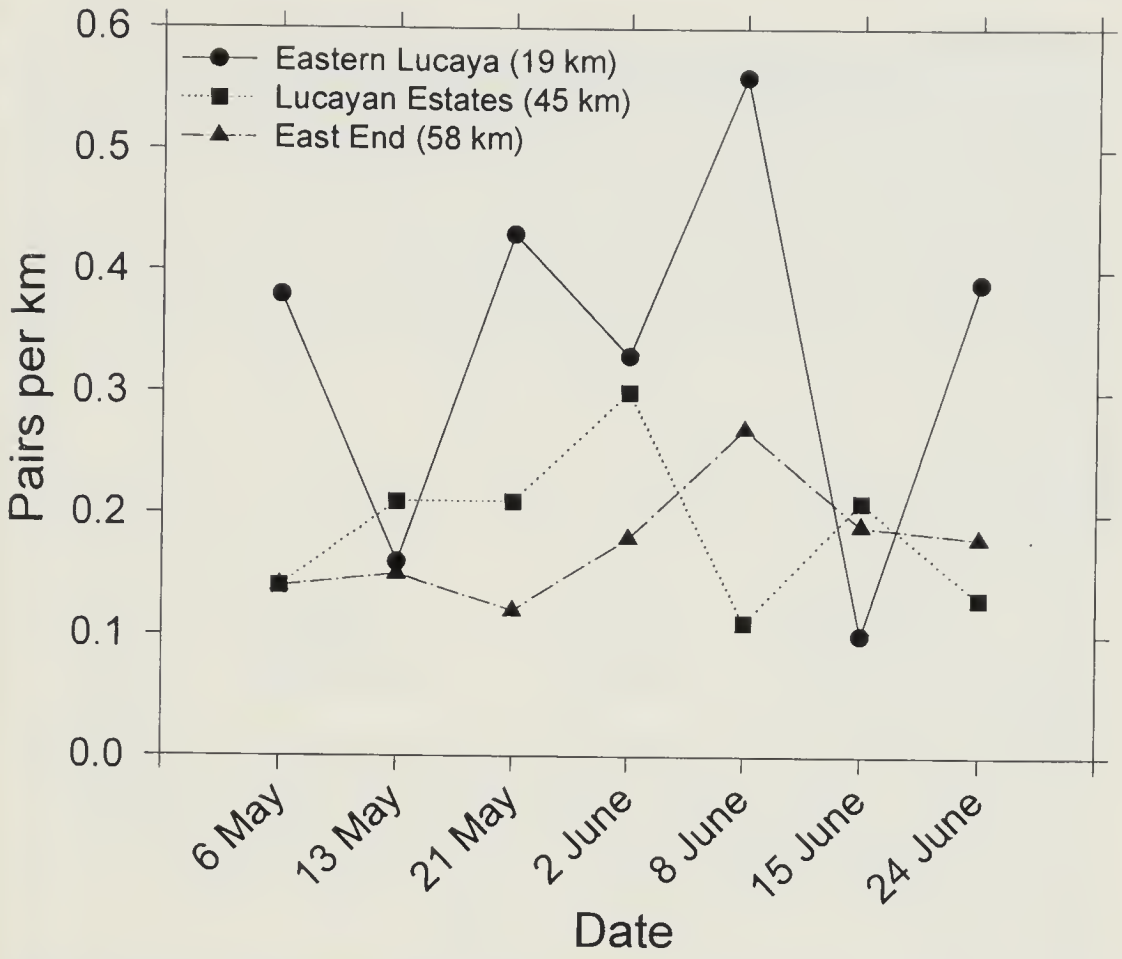

FIG. 3. Bahama Swallow pairs-km^{-1} from each of three survey routes sampled on three roughly consecutive days. Date is the day that the second route was sampled. The large variance of sightings on the Eastern Lucaya route is probably due to its shorter length.

result of the 1995 Andros survey roughly corresponds to the results of surveys on Grand Bahama near the same time (0.20 pairs-km^{-1} for 21 May and 0.25 pairs-km^{-1} for 2 June), it seems likely that the 1995 Andros results may be a reasonable index of the Andros population.

Conclusion.—Like many other species, the greatest threat the Bahama Swallow faces probably is habitat destruction. The most likely cause of major habitat alteration loss in the Bahamas will be logging, especially since much of the secondary forest is now becoming mature after the last spate of harvesting. However, another source of major habitat loss will be from housing development, particularly when the residential retirement and resort communities planned for Grand Bahama are more fully implemented. According to promotional brochures, these subdivisions are to house over 500,000 people and cover about 170 km^2 (P. Allen, unpubl. data), most of which is currently forested. This area was not included in

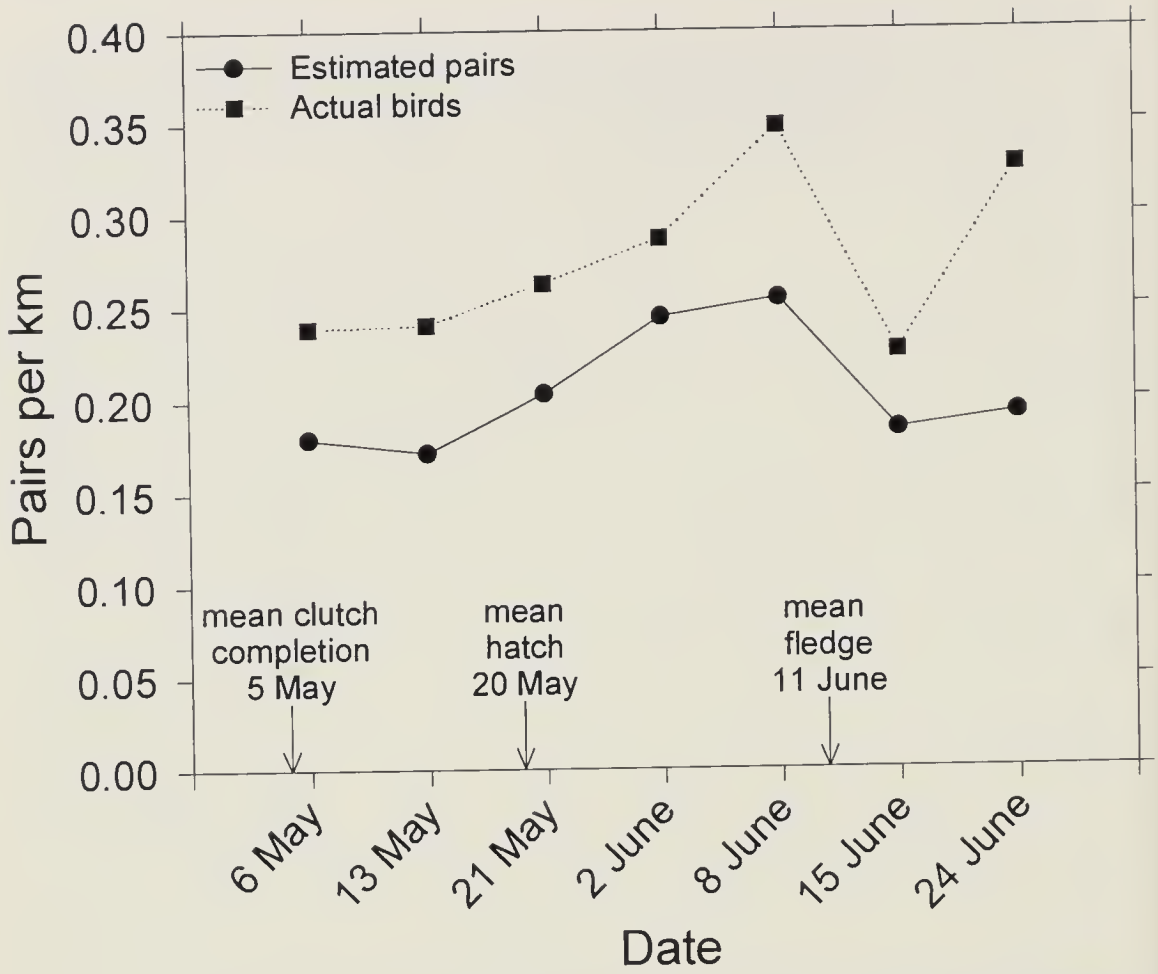

FIG. 4. Survey results combining the three routes of each survey using actual number of birds sighted (dashed line) or estimated number of pairs sighted (solid line). Date is the day that the second route was sampled.

the pine forest inventory by Allan (1986), but its development will effectively eliminate about 8% of the breeding habitat currently available to Bahama Swallows. Hurricanes pose another threat to Bahama Swallow habitat since they can demolish large portions of the forest on individual islands and have done so before in the Bahamas. However, if habitat loss from all sources can be minimized, and possibly mitigated through conservation measures such as nest box and snag management programs, the Bahama Swallow does not seem likely to become endangered. But, given the limited area of pine forest and the vulnerability of that habitat to human alteration, it seems unlikely that the conservation status of the species could ever be upgraded from its current near-threatened status.

ACKNOWLEDGMENTS

Lori Bushway, John Confer, Rick and Kathy Oliver, Bill Smith, and David Winkler provided support and advice that made this project possible. Nancy Jones furnished housing

and some transportation for the field work. Lori Bushway gave valuable field assistance and encouragement. Chuck Cavender provided logistical and field assistance on Andros. Philmore Russell and Edward Robinson also aided me in the field. I am grateful to the many landowners who gave me access to their property, especially to the Ministry of Public Works and Local Government for access to the Missile Base. I thank David Winkler for use of his Tree Swallow data. Tom Martin, Bill Smith, Bridget Stutchbury, David Winkler, and an anonymous reviewer provided comments which improved this manuscript. This study was funded by the Lincoln Park Zoo Scott Neotropic Fund, a Kathleen S. Anderson Award from Manomet Observatory, the North American Bluebird Society, the Purple Martin Conservation Association, and the Association of Field Ornithologists.

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Wilson Bull., 108(3), 1996, pp. 496–506

NEOTROPICAL MIGRATORY BREEDING BIRD COMMUNITIES IN RIPARIAN FORESTS OF DIFFERENT WIDTHS ALONG THE ALTAMAHA RIVER, GEORGIA

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ABSTRACT.—We surveyed riparian forest corridors of different widths along the lower Altamaha River in Georgia in 1993 and 1994 to investigate the relationship between forest corridor width and Neotropical breeding bird community diversity and abundance. Species richness and abundance of three of six focal species increased with increasing forest corridor width. We suggest if Neotropical breeding bird communities are a target group, that land managers should consider leaving a 100 m buffer strip along riparian zones. *Received 28 Aug. 1995, accepted 13 Feb. 1996.*

Studies of the effects of forest fragmentation (Whitcomb et al. 1981, Lynch and Whigham 1984, Robbins et al. 1989) on communities of breeding birds in discrete forest blocks of different sizes have suggested that many Neotropical migratory bird species are sensitive to a reduction in forest area. More difficult to assess is the effect of reduction in width of riverine forest corridors on bird populations; although forest area may be reduced by encroachment from the corridor edge, these forests often remain contiguous with wider sections of the corridor. Stauffer and Best (1980) found that bird species richness increased from about 10–30 species with increasing width in wooded riparian habitats ranging from 10–200 m wide in Iowa. They noted, however, that seven of 17 species previously thought to be area sensitive bred in buffers ≤20 m wide. In a study of breeding birds in wooded riparian zones in Maryland and Delaware, Keller et al. (1993) found that Neotropical migrants were more area sensitive than were either short distance migrants or residents. Neotropical migrants increased in richness as corridor width increased, particularly in corridors <200 m, while richness of the other bird groups remained relatively stable. Darveau et al. (1995) examined bird densities in riparian boreal forest corridors of different widths (20–300 m) which were bordered by recent (<2 yrs old) clearcuts. They found that forest-breeding birds were sensitive to corridor width and concluded that 60-m wide corridors were required to maintain forest breeding birds. In all of these studies, the riparian zones were usually bordered by agricultural or clearcut fields. Studies in which the riparian zone is bordered by pine

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silviculture are apparently lacking. The adjacent habitat could conceivably ameliorate the species-area effect because the pine plantation might support some birds that would otherwise be absent in an agricultural or clear-cut landscape.

In the southeastern United States, forested wetlands are being lost or converted to pine silviculture at an alarming rate (Winger 1986, Hefner et al. 1994). However, at present, land managers have no information about how wide a buffer strip adjacent to streams is necessary to maintain functional breeding bird communities. Understanding bird-habitat relationships is important both locally and over broad areas because forest health may depend on the presence of breeding birds. Forest-dwelling birds have been shown to control the numbers of insects feeding on tree foliage (Marquis and Whelan 1994). Further, recreation dollars associated with more natural forests are becoming a consideration in forest management (Wiedner and Kerlinger 1990, Kerlinger 1993).

We investigated the relationship between width of bottomland hardwood forest corridors along the Altamaha River in Georgia and breeding populations of Neotropical migratory birds. Our objectives were to examine the relationship between forest corridor width and bird species richness, density, and the probability of encountering a particular bird species.

STUDY AREA AND METHODS

We studied birds on the Altamaha River floodplain swamp, which begins at the confluence of the Ocmulgee and Oconee rivers at river km 212 in Montgomery and Jeff Davis counties, Georgia. These forests extend downstream to the Buffalo and Clayhole swamps at approximately river km 24 in Glynn and McIntosh counties. The three dominant community types sampled were: willow oak (*Quercus phellos*), overcup oak (*Q. lyrata*)-water hickory (*Carya aquatica*), and bald cypress (*Taxodium distichum*)-water tupelo (*Nyssa aquatica*) (Allard 1990). The first was a wet-mesic river floodplain forest dominated either by willow oak or laurel oak (*Q. laurifolia*), with several other hardwoods and bald cypress occurring in the canopy. The second was a wet river floodplain forest dominated in the canopy by overcup oak and water hickory. The third, a forested riverine swamp, was dominated by bald cypress and either water tupelo or Ogeechee lime (*N. ogeche*) in the canopy and was flooded for most of the year. Some small stream corridors were sampled which were swamp forests with the same floristic components as riverine bottomlands but with narrower zonation and less frequent flooding.

Variable length transects were placed perpendicular to the river, based on corridor width, shape, lack of disturbance, and presence of adjacent pine plantations. Riverine forest corridors were rejected if they had been extensively thinned or were in an early successional stage (trees <8 cm dbh), excessively convoluted at the pine plantation edge, within 100 m of other large forest tracts, or in close proximity to a major highway. Transects were located ≥500 m apart. Three corridor-width classes were used: narrow (<350 m), medium (400–700 m), and wide (>1000 m). Generally the Altamaha River meandered within a fairly defined (about 1500 m wide) bottomland which was bordered by pine plantations. Thus,

TABLE 1

NEOTROPICAL MIGRATORY BREEDING BIRDS KNOWN TO BREED IN SOUTH ATLANTIC COASTAL PLAIN FORESTS (ADAPTED FROM GAUTHREAUX 1992)[a]

Common Name (Scientific Name)
American Swallow-tailed Kite* (*Elanoides forficatus*)
Mississippi Kite (*Ictinia mississippiensis*)
Broad-winged Hawk (*Buteo platypterus*)
Yellow-billed Cuckoo (*Coccyzus americanus*)
Ruby-throated Hummingbird (*Archilochus colubris*)
Eastern Wood-Pewee* (*Contopus virens*)
Acadian Flycatcher (*Empidonax virescens*)
Great Crested Flycatcher (*Myiarchus crinitus*)
Blue-gray Gnatcatcher (*Polioptila caerulea*)
Wood Thrush (*Hylocichla mustelina*)
White-eyed Vireo (*Vireo griseus*)
Yellow-throated Vireo (*V. flavifrons*)
Red-eyed Vireo (*V. olivaceus*)
Northern Parula (*Parula americana*)
Yellow-throated Warbler (*Dendroica dominica*)
Prothonotary Warbler (*Protonotaria citrea*)
Swainson's Warbler (*Limnothlypis swainsonii*)
Louisiana Waterthrush (*Seiurus motacilla*)
Kentucky Warbler (*Oporornis formosus*)
Hooded Warbler (*Wilsonia citrina*)
Summer Tanager (*Piranga rubra*)

[a]Those species marked with an asterisk (*) were not recorded in sampling for the present study, although they were noted during other field work in the Altamaha River basin in 1993 or 1994.

when a wide corridor transect was chosen, the corridor width on the other side of the river tended to be narrow and vice versa. The Altamaha River, which usually exceeded 100 m in width, seemed to act as an effective barrier against cross stream movement of five of our focal species (MFH, unpubl. data). The only exception was the Prothonotary Warbler (scientific names in Table 1) which was observed frequently flying across the river. We selected 10 transect sites in 1993: four narrow (36–135 m), three medium (480–660 m), and three wide (1320–2088 m). From one to seven points were located along these transects for a total of 31 points. Points were located 50 m from the pine plantation edge and at 200 m intervals thereafter. Most transects were located in forested riverine swamps and wet and wet-mesic river floodplain forests. Exceptions included three narrow transects in which relatively steep (>30% slope) mesic bluff forests were part of the forest corridor.

In 1994, we sampled six of the 10 transects used in 1993, and 16 additional transects were added. Two medium and two wide transects sampled in 1993 were deleted because of marginal habitat characteristics. New transects added in 1994 included 14 narrow transects located in small stream corridors closely associated with the Altamaha River, one medium transect, and one wide transect. Totals for 1994 were 18 narrow (36–330 m), two medium (440–510 m), and two wide (1320–1512 m) transects, with 38 points surveyed.

We used the variable circular plot technique (Reynolds et al. 1980) to sample birds at points along each transect. In 1993, each point was sampled three times during 16–31 May,

1–15 June and 16–30 June. Sampling was confined to the first two periods in 1994. MFH was the only observer for all sampling. Order of sampling was stratified so that each point was sampled at least once within 1.5 h after sunrise. All sampling occurred within 4 h after sunrise.

All birds heard or seen during a 10-min sampling period were recorded, although only Neotropical migrants were used in these analyses (Table 1). We summed the number of species recorded at all points by corridor width to estimate species richness.

We recorded bird numbers at three distances: <25 m, 25–50 m, and >50 m. Each species had a maximum detectable range determined by calculating the ratio of birds per unit area within 50 m of the counting point to birds per unit area beyond 50 m and solving for the unknown area. The cut-off points for the species used in density estimates were Acadian Flycatcher—70 m, Blue-gray Gnatcatcher—50 m, White-eyed Vireo—80 m, Red-eyed Vireo—80 m, Northern Parula—80 m, and Prothonotary Warbler—100 m.

The structure of the plant community was sampled along each transect at five points at 10 m intervals on either side of each sampling point (10 points total for each sampling point). Percent canopy cover (>3 m height) and shrub cover (1–3 m height) were estimated using an ocular tube. The plant community type at each sampling point was deduced from plant species lists compiled at each sampling point (Allard 1990). We estimated the timber basal area at the sampling point with a cruising angle. Landsat TM and SPOT satellite imagery were used to measure the width of the forest corridor from river to pine plantation edge for each transect.

We estimated density per ha by corridor width and year for each species with sufficient data. Data consisted of the single count (3 in 1993, 2 in 1994) which had the highest number of birds detected. Densities of Neotropical migrants were estimated using the program DISTANCE (Laake et al. 1993). Three models (uniform, half-normal, hazard-rate) were evaluated using likelihood ratio tests to determine which model best fit the data. Once the final model was selected, we tested for annual differences in densities of each species within each corridor width by determining if the 95% confidence limits overlapped. We also tested for annual effects by fitting a nested logistic regression (PROC LOGISTIC, SAS 1990) model with corridor width and year effects versus corridor width only. The response variable was presence/absence of each species. Model selection was based on Akaike's information criterion (Akaike 1973).

Sensitivity to corridor width was examined using logistic regression (PROC LOGISTIC, SAS 1990). To produce a data set comparable to that of Keller et al. (1993) who sampled at the center of each riparian corridor, we subsampled those data taken from the approximate middle of each transect. At these points, a presence/absence data set was produced for each species. This response variable was then modelled, using corridor width as a predictor. Based on the parameter estimates, we calculated the estimated probability of a species occurring in a corridor of given width (PROC LOGISTIC, SAS 1990:1076).

Next, we examined whether species density was more closely related to the vegetative characteristics within the corridors or to corridor width alone. Because correlations were noted among vegetation measurements (unpubl. data), we reduced the three vegetation variables (percent canopy cover, percent shrub cover, timber basal area) into two variables (PC1, PC2) using principal components analysis (PROC PRINCOMP, SAS 1990). We then modelled the response variable, density of each species at a point, with the predictor variables corridor width, distance from the pine edge, PC1, and PC2 (PROC GLM, SAS 1990). To insure that birds were not responding to inherent differences in the vegetation among corridor widths, we examined the relationships among corridor width class and the predictor variables PC1 and PC2 by year and across years.

Finally, we examined the relationship between species richness and corridor width using

a generalized linear model (PROC GLM, SAS 1990) with year, corridor width, and year*corridor width as predictors.

RESULTS

We detected 48 bird species on the surveys, of which 19 were Neotropical migratory breeding birds (Table 1). Species richness ranged from four to 15 across all corridor widths with 4–14 in narrow, 11–13 in medium, and 12–15 in wide corridors. The third sampling period in 1993 did not add any unique species to measurement of species richness beyond those observed during the first two sampling periods. Species richness varied by corridor width and year ($F_{1,31} = 3.48$, $P = 0.07$), with narrow corridors having lower mean species richness (7.8 ± 2.48 SD) than either medium (12.0 ± 0.71) or wide (12.6 ± 1.52) corridors ($P < 0.05$). More species were recorded in 1993 than in 1994 ($F_{1,31} = 10.94$, $P = 0.002$).

Six species occurred in sufficient numbers to estimate their densities: Acadian Flycatcher, Blue-gray Gnatcatcher, White-eyed Vireo, Red-eyed Vireo, Northern Parula, and Prothonotary Warbler. The highest counts always occurred during the second survey, followed by the first survey, and finally the third survey. The third survey in 1993 added little to the results. There were no differences in densities of any species between years in either the medium or wide corridors ($P > 0.05$). Comparing all narrow corridors, densities of Acadian Flycatcher, Blue-gray Gnatcatcher, White-eyed Vireo, and Northern Parula in 1994 were lower than in 1993 ($P < 0.05$). Examining just those narrow transects surveyed in both years (versus examining all narrow transects surveyed in both years), no differences in densities were found between years ($P > 0.05$). Apparently, the new transects sampled in 1994 were responsible for the overall differences in densities between years for the narrow corridors. Thus, we believe that the differences between densities for the 1993 and 1994 narrow transects reflected habitat differences rather than annual differences. Those narrow transects added in 1994 were in small stream corridors closely associated with the Altamaha River, unlike the exclusively riverine corridors used in 1993. Logistic regression indicated that only the White-eyed Vireo demonstrated a difference ($P < 0.05$) in presence/absence between years, with fewer White-eyed Vireos being seen in 1994. Based on the combination of these two tests, we believe that there was no strong evidence for an effect of year on densities for these six species. Thus we combined data from both years in subsequent analyses.

For all six species, densities were higher in medium corridors than in either narrow or wide corridors (Table 2). However, the differences in

TABLE 2

DENSITY ESTIMATES PER HECTARE AND 95% CONFIDENCE INTERVALS OF SIX FOCAL SPECIES OF NEOTROPICAL MIGRATORY BREEDING BIRDS BY CORRIDOR WIDTH (CW), ALTAMAHA RIVER BASIN, 1993 AND 1994[a]

Species	CW[b]	Est. density	Confidence interval
Acadian Flycatcher	N	0.08	0.05–0.15
	M	0.10	0.08–0.12
	W	0.05	0.04–0.07
Blue-gray Gnatcatcher	N	0.07	0.04–0.15
	M	0.11	0.08–0.15
	W	0.08	0.04–0.17
White-eyed Vireo	N	0.06	0.04–0.10
	M	0.12	0.06–0.22*
	W	0.06	0.04–0.09
Red-eyed Vireo	N	0.08	0.04–0.14
	M	0.16	0.13–0.21
	W	0.06	0.05–0.07
Northern Parula	N	0.09	0.05–0.16
	M	0.22	0.16–0.31*
	W	0.07	0.06–0.08
Prothonotary Warbler	N	0.03	0.01–0.05
	M	0.07	0.04–0.13
	W	0.05	0.04–0.07

[a] An asterisk (*) denotes that the density estimate is significantly ($P < 0.05$) different than either of the other density estimates for that species.

[b] N = narrow corridors; M = medium corridors; W = wide corridors.

density were significant ($P < 0.05$) only for White-eyed Vireos and Northern Parulas.

Northern Parulas, White-eyed Vireos and Red-eyed Vireos exhibited significant relationships between corridor width and probability of occurrence ($P < 0.05$, Fig. 1). The response to increasing corridor width was most pronounced between 50 and 100 m. There was a greater than 80% chance of five of the six species, excluding Prothonotary Warbler, being detected in a 100 m wide corridor strip. Although not significantly so, both the Blue-gray Gnatcatcher and the Prothonotary Warbler were more likely to be found in wider corridors, whereas the Acadian Flycatcher was less likely to be found in wider corridors (Fig. 1).

PC1 and PC2 had eigenvalues >1 which is the usual cut-off point for inclusion in analyses such as ours (Nichols 1977). PC1 accounted for 36% of the variation in the three vegetation variables, while PC2 accounted for 32% for a cumulative accounting of 68% of the variation in vegetation variables. PC1 was positively associated with timber basal area and canopy cover and negatively associated with shrub cover. We

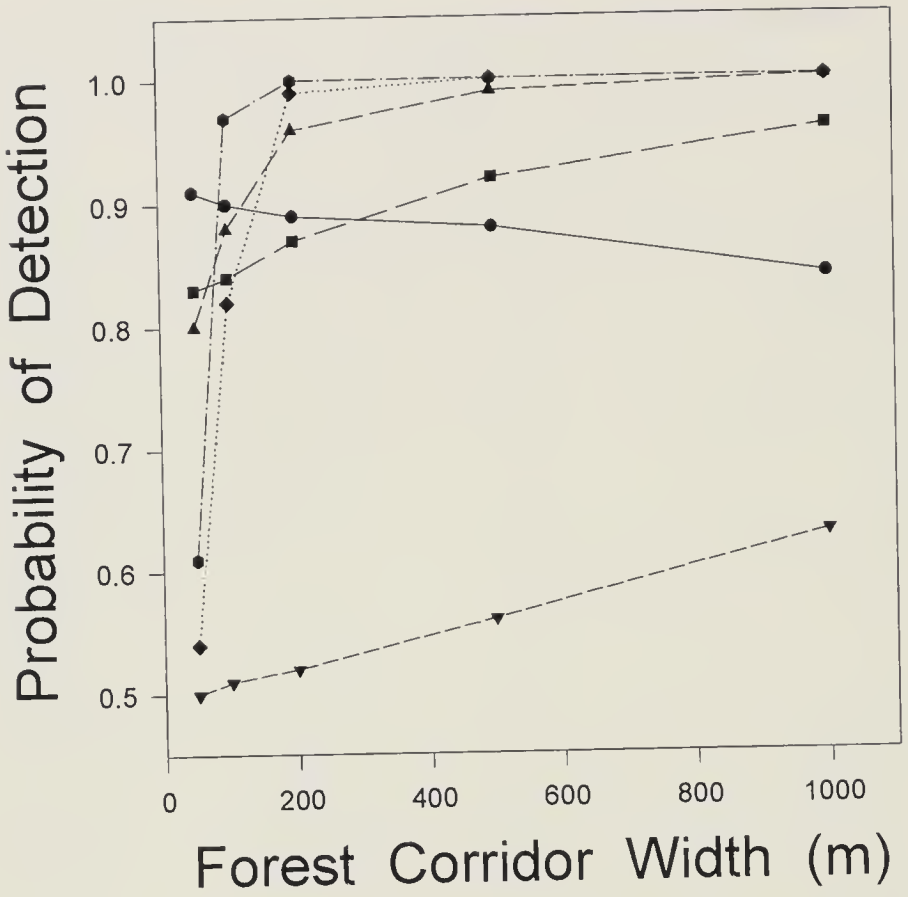

FIG. 1. Probability of detecting six focal species of migratory breeding birds along the Altamaha River riparian forest corridor. Solid circle—Acadian Flycatcher, square—Blue-gray Gnatcatcher, triangle (point up)—Northern Parula, triangle (point down)—Prothonotary Warbler, diamond— Red-eyed Vireo, hexagon—White-eyed Vireo. Points represent estimated probabilities of detection at 50, 100, 200, 500, and 1000 m corridor widths.

interpret this score, when high, as reflecting forest stands with a relatively closed canopy and little undergrowth. PC2 was positively associated with canopy cover and shrub cover reflecting forests with closed canopies and more undergrowth. Species-specific modelling revealed that Prothonotary Warbler and Red-eyed Vireo densities were positively related to PC1 ($P < 0.05$), while White-eyed Vireo density was negatively related to PC1 ($P < 0.05$). In addition, the density of Red-eyed Vireos was related positively to the distance from the pine-plantation edge ($P < 0.05$), while White-eyed Vireo abundance was positively related to corridor width ($P < 0.05$).

We found that vegetation structure differed by corridor width in 1993 ($F_{2,16} = 4.02$, $P = 0.04$) but not in 1994 ($F_{2,37} = 2.64$, $P = 0.09$). In 1993, the difference in vegetation structure was due to PC2, the amount of shrub cover. Combining years, there was no difference in vegetation structure ($F_{2,54} = 1.97$, $P = 0.15$).

DISCUSSION

The Neotropical migratory breeding bird community that we sampled along the Altamaha River was typical of what would be expected in the southeastern United States (Table 1; Hamel 1992). Only two species of Neotropical migrants were absent from our surveys, American Swallow-tailed Kite and the Eastern Wood-Pewee. The former probably has one of the lowest densities among breeding birds of Altamaha River bottomland forests, while the latter is not found in bottomland habitats in our area, preferring mature pine woodlands (MFH, pers. obs., Hamel 1992). Although the bird community that we monitored was typical, we point out that the Altamaha River and its associated riparian zone are not typical of the southeastern United States. The Altamaha River has the largest watershed in the Southeast (Anonymous 1986) and is famous for its extensive associated tracts of unbroken bottomland hardwoods (Wharton et al. 1982). Clearly these forested tracts are unusual today, and so our findings may not be entirely applicable to other riverine systems in the Southeast.

Species richness values by corridor width increased with area as Keller et al. (1993) found. The year effect we observed was, in part, a result of incorporating small stream corridors in 1994 which had, across the board, lower species richness values. Despite these differences in habitat types, all corridor widths had lower species richness in 1994; we are unsure why.

Of the six species for which we could estimate the probability of detection, five exhibited a trend towards increasing detection with increasing forest corridor width, three significantly so. Four of these species, Acadian Flycatcher, Prothonotary Warbler, White-eyed Vireo, and Red-eyed Vireo showed the strongest relationship between probability of detection and increasing forest corridor width (Keller et al. 1993). Keller et al.'s (1993) evidence for the Acadian Flycatcher was opposite from ours though, as we found Acadian Flycatchers tended to decrease in abundance with increasing corridor width (although not significantly). Robbins et al. (1989) and Dawson et al. (1993) both found the Acadian Flycatcher to be area sensitive (positively) in non-riparian forested situations in Maryland. The Prothonotary Warbler was area sensitive (positively) for Keller et al. (1993) but not for Robbins et al. (1989) or us.

The relationship observed between densities of the six species and corridor width was unexpected. We had anticipated that the highest densities would have occurred in the widest corridors, assuming that the widest corridors would have contained not only more total habitat but also habitat of higher quality. Our finding that vegetation structure was not consis-

tently related to corridor width indicated that wider corridors were not structurally different than narrower corridors. Despite the lack of differences in habitat structure that we measured, the differences in densities suggest either that differences in habitat quality existed, which we did not measure, or behavioral factors excluded some birds from the widest corridors. As Van Horne (1983) and Pulliam (1988) have asserted, high animal densities may result from excessive numbers of immigrants who have been forced away from the preferred habitat by higher ranking (more dominant) individuals. If true, then the lower densities in the widest corridors might reflect a predominance of more successful, more dominant individuals who benefit by controlling densities.

In the generalized linear model examining sensitivity to corridor width, vegetation parameters, and distance to pine edge, White-eyed Vireo was the only species whose numbers clearly showed a positive association with corridor width. During the breeding season, this species is not restricted to forest interiors; it frequently uses young second growth and other shrubby habitats. White-eyed Vireo's negative associations with canopy density and basal area and positive association with shrub density are easier to predict (Hamel 1992). Other studies (Robbins et al. 1989) have noted sensitivity to forest area for species common in our area, such as Acadian Flycatcher and Northern Parula. The much larger data set of Robbins et al. (1989) may have contributed to their better rate of detection of significant positive associations with forest area. Red-eyed Vireo numbers showed a positive association with distance from the pine-plantation edge, indicating a preference for forest interiors, and a preference for closed canopies, the latter having been noted previously (Robbins et al. 1989).

The rapid increase in probability of occurrence and species richness with increasing corridor width and the apparent asymptotic shape of the species abundance-area curves suggests that forest corridors of about 100 m should be sufficient to maintain functional assemblages of the six most common species of breeding neotropical migratory birds. This guideline exceeds the 60 m recommended by Darveau et al. (1995), but comparing boreal forests and southeastern bottomland hardwoods may not be appropriate. Our guideline does concur with the findings of Keller et al. (1993) who also recommended a 100 m wide corridor be maintained. Our recommendation does not take into account the needs of the least common species of Neotropical migratory birds encountered, which we were not able to ascertain from these data.

The value of corridors goes beyond the maintenance of breeding bird communities, as Naiman et al. (1993:209) concluded that "effective riparian management could ameliorate many ecological issues related to

land use and environmental quality." More specifically, Winger (1986) demonstrated that functional forested corridors assimilate nutrients and organic matter, hasten the degradation of persistent pesticides and decrease the bioavailability of heavy metals. Justification of streamiside corridors thus goes beyond breeding bird communities alone (see also Brinson et al. 1981).

ACKNOWLEDGMENTS

We thank R. Goodloe, C. S. Robbins, D. K. Dawson, and an anonymous reviewer for their comments on this manuscript. Funding was provided by The Nature Conservancy, the U.S. Fish and Wildlife Service, and the National Biological Service.

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Wilson Bull., 108(3), 1996, pp. 507–515

DAWN AND DUSK SINGING OF MALE AMERICAN ROBINS IN RELATION TO FEMALE BEHAVIOR

TORE SLAGSVOLD

ABSTRACT.—It has been assumed that females are particularly fertile during the first hour after laying when the next egg to be laid is fertilized. In many passerine birds, egg laying occurs early in the morning. Hence, it may be particularly important for males to sing at dawn to attract the mate and other females and to repel potential cuckolders. I studied song activity of mated male American Robins (*Turdus migratorius*). Egg laying occurred close to noon. However, males had a peak song activity at dawn but sang little around noon. Hence, the idea that mated males sing primarily to deter other males just before the 'fertilization window' was not supported. Male song activity tended to increase when the mate visited the nest during the day but less so when she entered the nest to roost at night. Synchronous emergence of all females at dawn resulted in synchronous termination of the dawn chorus, whereas a more asynchronous pattern of nest visits by females during the day and in the evening resulted in asynchronous and scattered periods of song. *Received 21 Nov, 1995, accepted 22 Feb. 1996.*

In the breeding season, passerine birds typically have a peak song activity at dawn and dusk (Armstrong 1973) and, in addition, egg laying often occurs early in the morning. Females may be particularly fertile during the first hour after laying, when the next egg to be laid is fertilized (Birkhead and Møller 1991). Hence, males may be singing at dawn to attract the mate and other females and to repel potential cuckolders (Mace 1986, 1987a; Cuthill and MacDonald 1990; Møller 1991). Such behavior has been reported in two hole nesting species, the Great Tit (*Parus major*; Mace 1986, 1987a, b) and the Willow Tit (*P. montanus*; Welling et al. 1995), although alternative explanations for dawn singing in these species also exist (see Slagsvold et al. 1994). I examined the possible relationship between song activity of male American Robins (*Turdus migratorius*) and female roosting behavior at dawn and dusk and female nest visiting behavior near the time of egg laying. Robins are interesting for several reasons. Egg laying does not occur at dawn but takes place in the middle of the day (Weatherhead et al. 1991, Scott 1993). Males guard their mates when fertile, suggesting that extra-pair copulations (EPCs) occur (Gowaty and Plissner 1987). I discuss how the results may help understand differences between species in daily variation of male song activity.

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METHODS

The study was conducted during 13–28 April 1994, in a mixed deciduous-coniferous woodland in St. Edward State Park near Seattle, Washington. The territories of 12 mated males were visited 20–70 min before the males started singing at dawn. In 10 cases, observations continued until noon. Observations were also made at 10 territories from 18:30 h until dark. Male song was recorded from a distance of 20–60 m, and one or two males were observed during each visit. Song activity was expressed as the percentage of minutes in which the male was heard singing (one or more times) of the total number of minutes of observation. Males were not banded but were identified by their proximity to the nests and to the females, their movements, song posts, and roosting sites.

Female robins may spend the night on the nest during the egg-laying period (Brackbill 1985, Slagsvold unpublished data). Video was used to record female presence on the nest, except at dawn when it was too dark. At dawn, the camera was not placed near the focal nest until the female had left. A Sony Handycam (CCD-TR805E) on a tripod was placed 3–8 m from the nest and pointed towards it. Female departure from the nest at dawn was observed in seven cases using 10× binoculars. In addition, the time of first appearance at the nest at dawn was recorded for another female that did not roost in the nest. Hence, I was able to examine the possible relationship between song activity and female emergence time for eight males. Three females were in the egg-laying period, four laid the final egg on the day of observation, and one was two days after termination of laying. Relative to the time of civil twilight, time of female emergence was not related to stage of breeding or date of observation (data not shown), and so the data were pooled. Civil twilight and sunrise and sunset times were for Seattle (Federal Office Building, Pacific Standard time, adjusted by one hour to represent summer time; "Climatology of the United States," no. 40–45, Washington, D.C., 1961).

The approximate time of egg laying was recorded by inspecting nests at variable hours of the day when the female was absent, and also by analyzing at which times the female was on and off according to the videofilms. Day 1 is defined as the day when the first egg was laid. Mean clutch size was 3.2 eggs (range 3–4, N = 9). Observations of dawn and dusk singing were carried out from Day −4 to Day 5. One nest was lost before egg laying had begun, so the precise stage of breeding was unknown.

RESULTS

In the morning, females left the nest/roost between 05:35–05:57 h ($\bar{x}$ = 05:50 ± 8 min [SD], N = 8), which was 9–19 min ($\bar{x}$ = 13 ± 3, N = 8) after civil twilight and 16–25 min ($\bar{x}$ = 21 ± 3, N = 8) before sunrise. After emergence, females were seen feeding on the ground. Those that had finished egg laying, or that laid the final egg later that morning, entered the nest to incubate earlier after sunrise ($\bar{x}$ = 3 ± 5 min, N = 3) than those that were still in the laying period ($\bar{x}$ = 142 ± 114, N = 4; z = −2.31, P = 0.021, U-test). The females spent 10–60 min ($\bar{x}$ = 31 ± 20, N = 6) on the nest on their first visit, followed by a period off of 10–105 min ($\bar{x}$ = 34 ± 34, N = 7) before a new period on. Hence, the synchronous behavior of the females at dawn, as measured by their emergence times, soon disappeared.

In the evening, females entered the nest to roost between 19:30–20:20

h ($\bar{x}$ = 20:01 ± 17 min, N = 8), which ranged from 33 before to 13 min after sunset ($\bar{x}$ = 4 ± 17, N = 8) and 20–67 min before civil twilight ($\bar{x}$ = 37 ± 17, N = 8). Variation among females was significantly greater for evening roosting times than for dawn emergence times, when considered relative to the times of sunset and sunrise, respectively (F = 32.9, df = 7,7, $P < 0.001$, Variance ratio test). Before entering the nest to roost at night, the females spent 10–38 min off ($\bar{x}$ = 18 ± 10, N = 7). Before this last period off, they had spent 10–48 min ($\bar{x}$ = 26 ± 15, N = 7) on the nest.

Assuming that laying occurred halfway between two nest inspections (Weatherhead et al. 1991), and using the median value for each female in case of observations of more than one egg laid (1–3 eggs per female), the median time of laying was 11:50 h (range 10:43–15:13, N = 9; $\bar{x}$ = 12:32 ± 88 min, if using mean of mean values). Including only cases when the interval between two nest inspections was less than 5 h, the median was 11:25 h (range 10:43–12:39, N = 6; $\bar{x}$ = 11:30 ± 42 min, if using mean of mean values). Using a similar method, an average laying time of 11:32 EDT was found in eastern Ontario, Canada (Weatherhead et al. 1991).

One copulation was observed. It occurred on the ground 8 m from the nest at 06:05 h on 18 April, 10 min after the female left the nest. Between 09:04 and 12:00 h on the same day, the female laid the third egg of a clutch of four. At another nest, a male tried to copulate with a female when she was sitting on the nest rim (at 08:23 h; recorded on video), but she moved away. Between 11:12 and 12:05 h on the same day, she laid the second egg of a clutch of three.

A peak in song activity occurred at dawn, with little singing thereafter (Fig. 1). One male did not sing at all at dawn before the female left the nest. Excluding this male, males started singing from 42 min before to 7 min after civil twilight ($\bar{x}$ = 12 ± 17 min before civil twilight, N = 11), or 5–56 min ($\bar{x}$ = 24 ± 21, N = 8) before the mate left the nest. Relative to the time of civil twilight, onset of dawn singing was not related to stage of breeding (Spearman, $r_s = -0.16$, P = 0.62, N = 11; stage of breeding measured as the number of days elapsing until the day of the final egg laid; data ranging from five days before this date to two days after). Because some males did not start singing until soon before female emergence, song activity did not peak until just before the female left the nest (Fig. 2). Song activity was low after female emergence (Fig. 2). Comparing a 10 min period before and after female emergence, song activity dropped for seven of eight males (no difference in one case; $z = -2.39$, P = 0.017, N = 7, Wilcoxon matched pairs test). When males started singing, the approximate mean distance between the nest and the

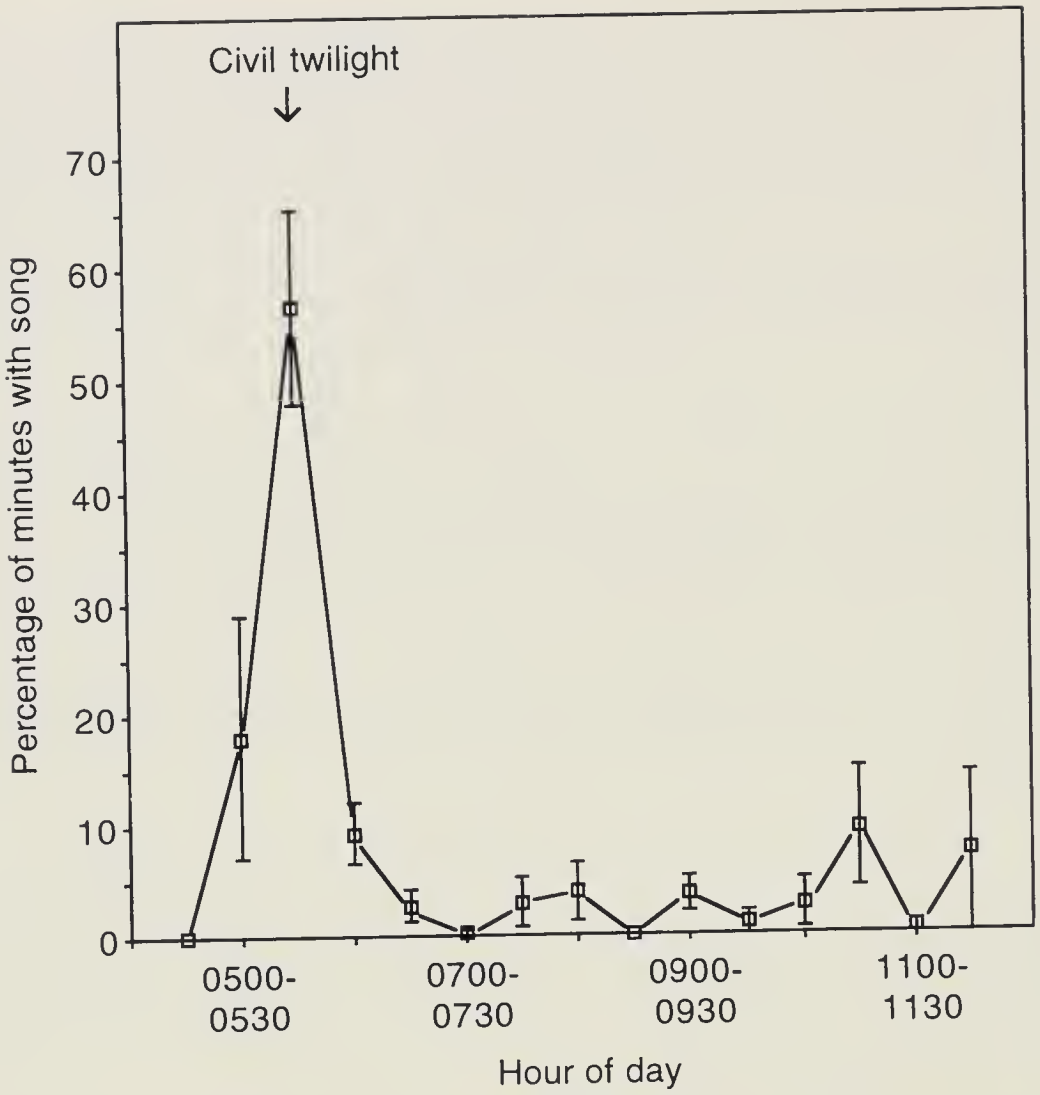

FIG. 1. Mean (±SE) song activity of ten male American Robins, calculated for consecutive 30-min periods from dawn to noon.

perch (distance along the ground) was 33 m (SD = 9, range 20–50, N = 11). Distance was not related to stage of breeding (r_s = 0.03, P = 0.92, N = 11). No males were seen flying to a nest before female emergence. However, later in the day (between 06:57–19:29 h), at least six males visited the nest without the females being present, and two males visited the nest to feed the mate.

Song activity was low between dawn and noon (Fig. 1) despite the fact that most eggs were laid around noon. I compared the data from all periods when the female was on the nest (1–6 periods combined for each male, $\bar{x}$ = 119 min of observation) with the data from all periods when the female was off the nest (1–7 periods combined for each male, $\bar{x}$ = 136 min of observation). Males (N = 9) were observed singing during

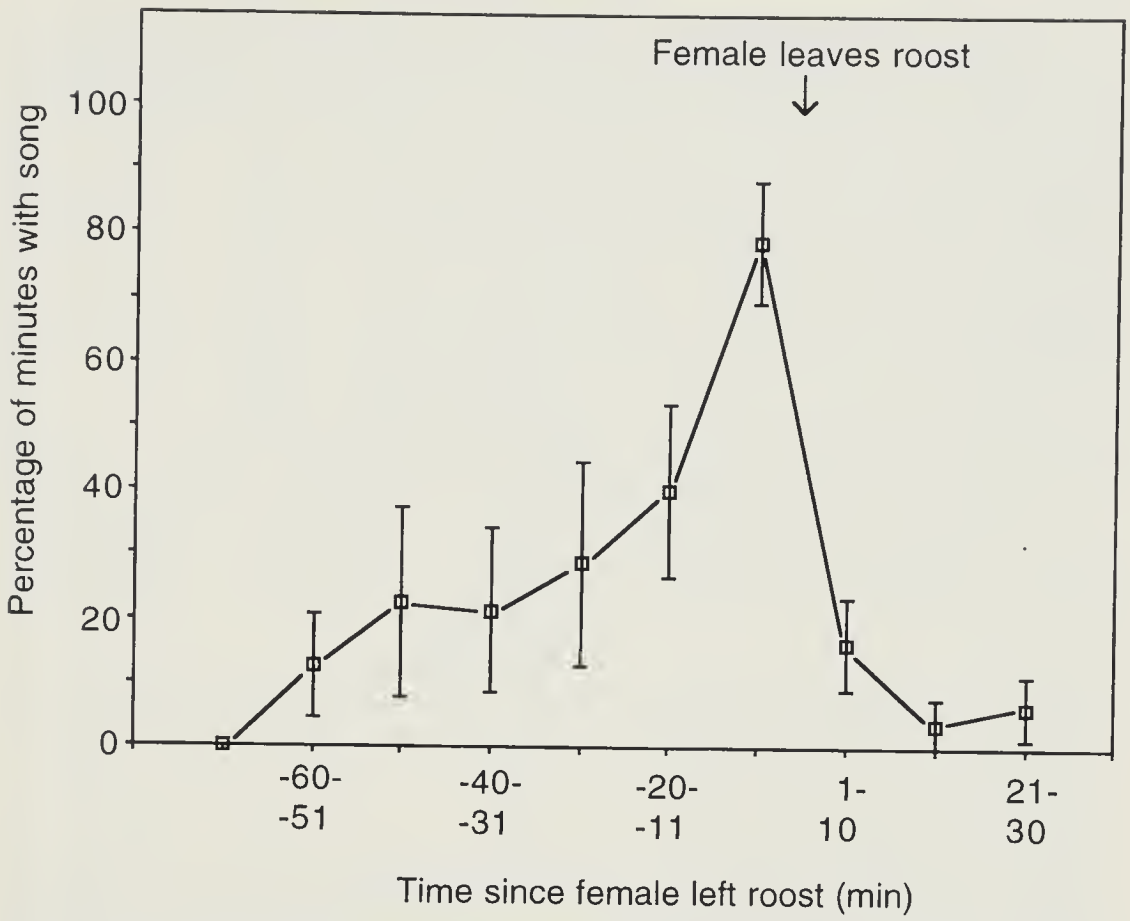

FIG. 2. Mean (+SE) song activity of eight male American Robins, calculated for consecutive 10-min periods before and after the female left her night roost at dawn.

0–17% ($\bar{x} = 5 \pm 6$) of the minutes when a mate was on the nest, and 0–4% ($\bar{x} = 1 \pm 2$) when she was off the nest. The difference was nearly significant ($z = -1.86$, N = 7, $P = 0.063$, Wilcoxon matched pairs test; two males did not sing at all).

Song activity of mated males was low in the evening (Fig. 3). After 18:30 h, three of the ten males included in Fig. 3 did not sing at all. The other seven males had only one or two periods of song during that period (separated by at least 10 min without song). The periods of singing lasted only 1–9 min ($\bar{x} = 4 \pm 3$, N = 7). When the female entered the nest to roost at night, two of seven males immediately started singing for eight and nine minutes, respectively. These were the longest song periods recorded of any mated male in the evening. The seven males that did sing after 1830 h stopped singing from 84 min before to 20 min after sunset ($\bar{x} = 21 \pm 35$ min before sunset) and 17 to 117 min before civil twilight ($\bar{x} = 54 \pm 35$).

Male (N = 7) song activity was recorded after 18:30 h and before the

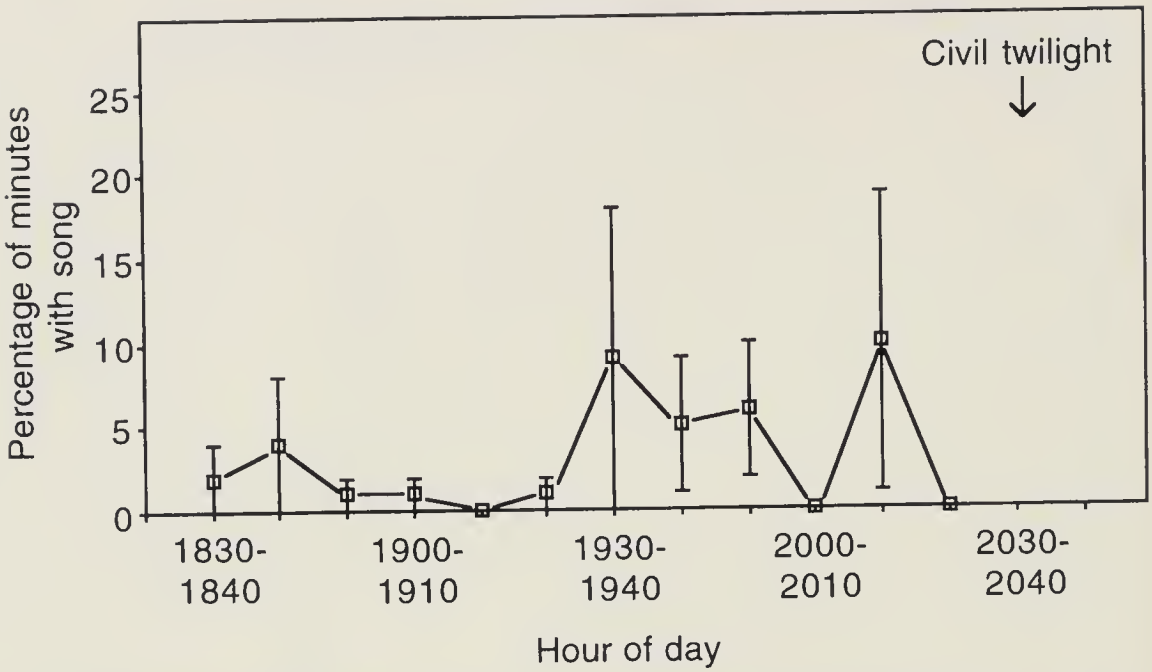

FIG. 3. Mean (+SE) song activity of ten male American Robins, calculated for consecutive 10-min periods in the evening.

final roosting time of the mate when the female was on the nest (1–3 periods combined per female, $\bar{x}$ = 36 min of observation) and when off the nest (1–3 periods combined per female, $\bar{x}$ = 51 min of observation). Song activity (percentage of minutes with male heard singing) was low in both cases (female on the nest: $\bar{x} = 1.1 \pm 1.9$; female off the nest: $\bar{x} = 0.6 \pm 1.7$; $z = -0.45$, $P = 0.65$, Wilcoxon matched pairs test).

DISCUSSION

Two important results were found. First, mated male robins exhibited peak song activity at dawn but sang little around the time of egg laying at noon. Hence, the hypothesis that mated males sing primarily to deter other males just before the "fertilization window" (Mace 1987a) was not supported. Second, song activity appeared to be influenced by female roosting behavior. Singing rates declined when the female left the night roost.

The principal function of dawn singing in mated male robins seems to have something to do with the female's being on the nest. Why should males be singing then? Dawn song may have several functions (see review in Slagsvold et al. 1994): (1) serve as pair-bond reinforcement and stimulate hormonally-mediated aspects of breeding in females; (2) tell the mate that she can emerge from the roost and nest without risk of predation and of revealing the location to nest predators; (3) attract the mate for

copulation; (4) attract a new mate in case the former mate has disappeared during the night; (5) attract other females for EPCs; (6) deter other males and so avoid that they will try to copulate with the mate; and (7) defend the nest site and the territory. The hypotheses are not mutually exclusive and may work in concert (Mace 1987b, Slagsvold et al. 1994). Further studies are needed to single out the relative importance of each.

The fact that male robins sang little close to the time of egg laying does not exclude the possibility that song is used as a mate guarding tactic. The only copulation seen occurred soon after the female left the roost at dawn, and so dawn singing may be related to this event. Although Weatherhead et al. (1991) suggested that robins lay eggs around noon because this may be a suitable time for copulation, no observations of copulations were reported. Gowaty and Plissner (1987), studying mate guarding in robins in the fertile period, observed copulations at all hours of the morning except for the hour after dawn; no observations were made after noon. However, few copulations were observed, and the authors did not report the actual frequencies. Further studies are needed to see if dawn is the regular time of within-pair copulation in robins as has been observed in some other passerine birds (Mace 1987a, Birkhead and Møller 1991, Davies 1992). In birds, females may actively seek EPCs with males of high quality (e.g., Kempenaers et al. 1992). No information exists on when and where EPCs take place in robins. However, as found in another passerine, the Great Reed Warbler (*Acrocephalus arundinaceus*; Hasselquist et al. 1995), they may prefer extra-pair mates with large song repertoires. In European Starlings (*Sturnus vulgaris*), females would only solicit copulation if the social or extra-pair mate sings (Eens and Pinxten 1990).

My results support those of others (e.g., Mace 1986, 1987a; Cuthill and MacDonald 1990; Pärt 1991; Otter and Ratcliffe 1993; Slagsvold et al. 1994; Welling et al. 1995) that male song activity is influenced by female behavior. Male robins start dawn singing about an hour or less before female emergence, as do male Great Tits, even though female Great Tits leave the roost, on average, 49 min later than female robins when measured relative to civil twilight (Slagsvold et al. 1994). In both species, males may increase song activity if the mate enters the nest during the day and at dusk. Hence, knowledge of factors that influence female roosting behavior may help explain differences in daily variation of male song activity within and between species of passerine birds. For instance, the fact that most of the males within a particular species, like the robin, stop singing more or less at a constant time in relation to light intensity at dawn, may not necessarily be related to a sensitivity of males to light per se but occur because this is the time when their mates leave

their respective roosts. When the emergence at dawn of female Great Tits was experimentally delayed, males continued singing for a longer period (Mace 1986).

Female robins left the roost, on average, 13 min after civil twilight, and the variation among females was low (range 9–19 min). At that time of the day, light intensity changes very fast, apparently synchronizing emergence. A more synchronous emergence in female robins than in female Great Tits (see Mace 1987b, Slagsvold et al. 1994) may also be due to the fact that robins do not lay an egg before leaving the night roost in contrast to the tits. Later in the morning, female behavior was more asynchronous, as were egg laying times, resulting in asynchronous periods of singing by males. In some other passerines, egg laying occurs in mid-morning and may be more synchronous than in robins, resulting in stronger synchronization of male song activity. In support of this idea, song activity of many passerine birds drops after a peak at dawn but reaches a new but lower peak later in the morning (Klockars 1941, Gyllin 1967, Lomholt 1971). One explanation for the initial drop is that males need to forage after dawn singing (Klockars 1941, Lomholt 1971). However, the drop may also reflect a more synchronous mate guarding by males early than late in the morning.

I conclude that to understand further daily variation in male song activity in passerine birds, more attention should be paid to the role of the females and, hence, on the factors that influence their copulation and roosting behavior. Information is needed concerning female emergence times at dawn and dusk and on the degree of synchronization of these events between females.

ACKNOWLEDGMENTS

I did this research during sabbatical year at the Burke Museum, Univ. of Washington. I thank S. Rohwer for arranging the stay in Seattle, J. Pillers for permission to work in St. Edward State Park, D. Hartmann for climatic data, P. K. Slagsvold for assistance in the field, and H. Lampe, G.-P. Sætre, and K. Yasukawa for comments on the manuscript. The study was supported by a grant from the Norwegian Research Council.

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Wilson Bull., 108(3), 1996, pp. 516–523

BREEDING BIOLOGY OF THE CRESTED CARACARA IN SOUTH TEXAS

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ABSTRACT.—We studied the breeding biology of six nesting pairs of Crested Caracaras (*Caracara plancus*) from January to August 1989 in Austin and Colorado Counties, south Texas. Four of the pairs nested in Macartney rose (*Rosa bracteata*). All nests were built below the nest-support canopy. We found caracaras laying eggs between 17 January and 23 June. Eggs hatched from February to April, and in June for two second nesting efforts. Young from successful first nesting efforts fledged from April to June. By August we did not see young or adults in the natal area. Nest building and courtship averaged 21 days (N = 2 pairs). Incubation periods averaged 30 days (N = 4 pairs), nestling dependency periods averaged 56 days (N = 5 pairs), and post-fledgling dependency periods averaged 33 days (N = 4 pairs). We believe that two of the pairs each laid a second clutch in June, but the newly-hatched chicks were killed by red imported fire ants (*Solenopsis invicta*). Overall nesting success was 45.7%. Success for first nesting attempts was 72.6%. *Received 7 Sept. 1995, accepted 13 Feb. 1996.*

In the United States, the Crested Caracara (*Caracara plancus*) primarily is found in Texas, Florida, and Arizona (Palmer 1988). The Florida population is listed as threatened under the Endangered Species Act (U.S. Fish and Wildlife Service 1987). Natural history of the Crested Caracara in North America has been described (Bent 1938, Brown and Amadon 1968, Oberholser 1974), but there has been little in-depth study of the species. Knowledge of the Texas population is limited to Oberholser (1974) and several brief notes. In general, little is known about the Crested Caracara's breeding biology. The lack of data on breeding biology precludes ability to make proper evaluations of population status and trends. Our objective was to describe the breeding biology, egg measurements, and nesting structures of the Crested Caracara in south Texas.

METHODS

We studied nesting pairs of Crested Caracaras in Austin and Colorado Counties, south Texas, from January 1989 to August 1989. The study area was centered on the Attwater Prairie Chicken National Wildlife Refuge (APCNWR), Colorado County (29°40′N, 96°15′W). The study area was at the western boundary of the Gulf Coast Prairie and the southern boundary of the Post Oak Savannah. The climax vegetation is tallgrass prairie characterized by big bluestem (*Andropogan gerardi*) and Indiangrass (*Sorghastrum nutans*) with overstory trees such as post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*) (Gould 1975). Invading shrubs include Macartney rose (*Rosa bracteata*), dewberry (*Rubus trivialis*), and yaupon (*Ilex vomitoira*) (Gould 1975).

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We located nests through aerial and ground surveys. Once we located a nest, we recorded the following information: nest-tree species and height, height of nest above ground, location of nest with respect to nest-tree canopy, and nest dimensions (length, width, internal bowl depth). When a nest was under construction or refurbishment, we recorded the materials used (species where possible), participation of each sex in nest-building, and duration of construction or refurbishment. We defined a nest as refurbished if we observed pairs adding material to an existing nest.

We divided the breeding season into courtship, incubation, nestling, and post-fledging dependency periods. The onset of courtship was the first day we observed a pair copulating. We defined post-fledging dependency as the period when juveniles were fed by the adults within 0.8 km of the nest. The end of the post-fledging dependency period was the date the young were last seen under these criteria. When we located a nest, we checked for eggs or nestlings. If there were no eggs or nestlings, we inspected nests daily with a mirror to determine onset of egg-laying. We determined the laying sequence by marking eggs with a soft lead pencil. We inspected each nest once a week to record any losses. At the completion of egg-laying, we recorded mass, length, and width of each egg.

Once we located a nest, we began observations of daily behavior of nesting pairs from sunrise to sunset. We observed each pair one day a week during the entire breeding season. Beginning three days before hatching (25 days after the onset of incubation) and three days before fledging (8 weeks after the onset of incubation), we inspected nests daily to record the initiation and sequence of hatching and fledging, respectively.

After the young hatched, we monitored nests at one-week intervals to check nestling survival and to record when young fledged. Nestling ages were estimated from plumage characteristics as described by Bent (1938) and Oberholser (1974). To facilitate monitoring young after fledging, we marked nestlings at approximately six weeks of age. Measurements and mass were taken for each nestling, and a U.S. Fish and Wildlife Service band was attached to its right leg. Nestlings were measured with a 24-cm ruler and a Mitutoya Model 550-633 caliper as described by Baldwin et al. (1931). Young were color-marked with a 7 cm-long blue, white, or pink vinyl plastic streamer attached to the left leg. Each streamer had an alphanumeric code painted on each side using NazDar, an ink formulated to fuse with vinyl surfaces. We were able to distinguish the sexes by size.

We estimated nesting success, using the method developed by Mayfield (1961, 1975) and a computer program created by J. L. Morrison. We calculated weekly survival for the incubation, nestling, and post-fledgling dependency periods and the total probability of nest success. We defined a nest as our sample unit and a successful nest as a nest in which at least one young survived to end of the respective period.

RESULTS

We found six caracara nests in various stages of development through 10 h of aerial and 400 h of ground surveys from late December to mid-July. Two nests were on the APCNWR and four were on private property. Five nests were in shrubs; four in Macartney rose and one in yaupon. One nest was in eastern red-cedar (*Juniperus virginiana*). All nests were constructed in the tallest shrub or tree in the immediate area. Measurement were taken on five nests, as the sixth (Nest 3) deteriorated before we could measure it. Nest trees averaged 4.3 ± 1.4 m (SE) in height, nests averaged 3.7 ± 1.2 m in height above ground, and the distance between the nest and the canopy averaged 55 ± 25 cm. Nests averaged 59 ± 5

TABLE 1
BREEDING CHRONOLOGY OF CRESTED CARACARAS, SOUTH TEXAS

Nest no.	Date found	Eggs laid		Eggs hatched		Nestlings fledged		Last seen fledglings
		Date	No.	Date	No.	Date	No.	
1-1[a]	10 Jan	17 Jan	2	13 Feb	1	9 Apr	1	17 May
1-2[b]		17 Jun	1	16 July	1[d]	—[e]	—	—
		18 Jun	1[c]	—		—	—	—
2[f]	21 Feb	12 Mar	2	—	—	—	—	—
3[g]	27 Mar	—	—	—	—	—	—	—
4	9 Mar	19 Mar	1	16 Apr	1	10 Jun	1	7 July
		21 Mar	1	18 Apr	1	12 Jun	1	7 July
5-1[a]	27 Mar	?	?	?	?	25 Apr	2	4 Jun
5-2[b]		24 Jun	2	23 July	2[h]	—	—	—
6	17 Mar	?	?	31 Mar	1	24 May	1	20 Jun
				1 Apr	1	24 May	1	20 Jun
				2 Apr	1	26 May	1	20 Jun

[a] Denotes first nesting attempt.
[b] Denotes second nesting attempt.
[c] Egg did not hatch.
[d] One nestling killed by red imported fire ants (*Solenopsis invicta*).
[e] No data.
[f] Adults abandoned nest at 31 days of incubation.
[g] Adults abandoned nest building after three days.
[h] Two nestlings killed by red imported fire ants (*S. invicta*).

cm in length, 50 ± 2 cm in width, and bowls averaged 11 ± 2 cm in depth. All nests were buried in the canopy and were impossible to see from the air or ground. Two of the nests constructed in Macartney rose could be entered and exited by the caracaras through only one opening in the foliage. Nests were constructed of Macartney rose, dewberry, yaupon, or broomweed (*Gutierrezia sarothrae*) twigs. Nests built in Macartney rose were almost exclusively built with that shrub's twigs.

Four nests were reused in the 1989 nesting season. Nests 4 and 6 were built by caracaras in 1988 (O. Benton, pers. comm.; J. Holtkamp, pers. comm.; respectively). Nests 1 and 5 had eggs laid in them in January and February 1989, respectively, and again in June 1989.

We observed breeding behavior from January through July (Table 1). We observed pairs copulating as early as 10 January and as late as 19 September. Pair 1 copulated four times during the nestling period (March and April), and Pair 4 copulated on 19 September, 100 d after the young had fledged. We observed courtship behavior during 12.5 ± 2.1 d (N = 6 pairs). The incubation, nestling, and post-fledging dependency periods averaged 29 ± 0.5 d (N = 3), 56.2 ± 0.4 d (N = 5), and 31.8 ± 2.5 d (N = 5) in length, respectively.

TABLE 2

MEASUREMENTS FROM SIX CRESTED CARACARA NESTLINGS AT VARIOUS STAGES OF DEVELOPMENT IN AUSTIN AND COLORADO COUNTIES, SOUTH TEXAS, 1989

Nest	ID	Age (days)	Wing chord (cm)	Tail (cm)	Tarsus (cm)	Hallux (cm)	Culmen (cm)	Mass (g)
1	A1	47	28	17	9	1.4	2.32	1100
4	D3	26	16	7	8.5	1.48	2.24	880
4	D3	45	29	16.5	9	1.57	2.49	960
4	E1	28	14	6.7	8	1.33	2.15	880
4	D1	47	29	17	8	1.7	2.67	960
6	A2	39	23	11	9.5	1.21	2.51	1200
6	A2	43	26.5	14	10	2.05	2.49	1220
6	D1	37	20.5	9.5	9	1.53	2.48	1160
6	D1	54	35	19	9	1.74	2.28	1160
6	A4	38	24	12	8	2.1	2.53	1100

Pairs laid eggs from January through June (N = 5) (Table 1). Pair 2 laid two eggs on 12 March but abandoned the eggs after 30 d of incubation. We opened the eggs and found them infertile. Pair 3 did not lay eggs, as the pair abandoned the nest on 29 March after 3 d of nest building. Pair 4 laid two eggs from 19 March to 21 March. We did not located Pair 6's nest in time to determine when the eggs were laid, but we observed three young hatch from 31 March to 2 April. Pairs 1 and 5 laid second clutchs. Pair 1 laid two eggs on 17 January and laid two eggs from 17 June to 18 June. Pair 5 fledged two young 25 April and laid two eggs on 24 June. One chick hatched in Nest 1 and two chicks hatched in Nest 2 on 16 July and 23 July, respectively. All three nestlings from these second clutches were killed by red imported fire ants (*Solenopsis invicta*).

Clutch size was determined for five nests; four nests had two eggs, and one nest had three eggs. Eggs were laid at 1–2 day intervals (N = 3 nests). Eggs averaged 53.1 ± 0.1 mm in length, 41.3 ± 0.03 mm in width, and 65.2 ± 0.6 g in mass (N = 4).

Young caracaras were found in the nest from late February to mid-June, and fledged from early April to mid-June (N = 8). The older chick always left the nest first. Time between fledglings leaving the nest was between 1–2 days (N = 5 fledglings). Measurements and masses were similar for nestlings of similar age (Table 2).

Total probability of nest success for nests initiated in January through March was 72.6% (N = 5), compared to 45.7% (N = 7) for all attempts (Table 3). We did not include Pair 3 in the calculation of nest success.

TABLE 3
NESTING SUCCESS FOR CRESTED CARACARAS IN AUSTIN AND COLORADO COUNTIES, SOUTH TEXAS, 1989

Mayfield estimate	Incubation	Nestling	Post-fledging dependency	Overall
	Earlier nests (Jan–Mar)			
Total nests observed	4 (3)[b]	4 (4)[b]	4 (4)[b]	—
Traditional success estimates	0.750	1.00	1.00	—
Total observed weekly exposure	13.0	28.0	32.0	—
Mayfield estimated weekly survival probabilities	0.923 ± 0.074[a]	1.00	1.00	—
Total probability of success (Mayfield)	0.726 ± 0.116[a]	1.00	1.00	0.726
	All nests (Jan–Jun)			
Total nests observed	6 (5)[b]	6 (4)[b]	4 (4)[b]	—
Traditional success estimates	0.833	0.666	1.00	—
Total observed weekly exposure	21.0	28.2	32.0	—
Mayfield estimated weekly survival probabilities	0.952 ± 0.046[a]	0.929 ± 0.048[a]	1.00	—
Probability of success for entire period	0.823 ± 0.083[a]	0.555 ± 0.082[a]	1.00	0.457 ± 0.140[a]

[a] Standard deviation.
[b] Number of successful nests is in parentheses.

We observed Pair 3 copulating and nest building for only three days before they left the study area.

By mid-August, young and adults were not regularly observed on or around the nest. On 19 September, the family group from Nest 4 was observed roosting on a powerline 2 km from the nest. Pair 6 was seen 2 km from the nest on 13 September.

DISCUSSION

We report several new findings from our research. Previously unreported for Crested Caracaras has been double brooding, fire ant predation on newly-hatched nestlings, body measurements and masses of nestlings, yaupon and eastern-red cedar as nest trees, and duration of the post-fledging dependency period. Pairs constructed nests from January to June. Simmons (1925) found nest materials collected as early as December in

Florida, and Levy (1961) observed nest construction in Arizona on 20 March. In this study, caracaras nested in tall, dense Macartney rose stands. Caracaras nested in the tallest vegetation in the area, Macartney rose on the APCNWR, and eastern red cedar on the Underwood Ranch. Previous accounts from North America reported caracaras nested in ebony (*Pithecollobium* spp.), hackberry (*Celtis* spp.), Macartney rose, mesquite (*Prosopis* spp.), oaks, palmettos (*Sabal* spp.), pines (*Pinus* spp.), saguaros, yuccas, and on cliffs (Bent 1938, Dillon 1961, Levy 1961, Oberholser 1974, Layne 1978, Farquhar 1986, Ellis et al. 1988). This is the first time yaupon and eastern-red cedar have been reported as nest supports.

Nest heights were similar to those reported by Oberholser (1974). In this study caracaras built their nests below the nest-support canopy. Caracaras may prefer their nests below the canopy rather than on top. Only Bent (1938) and Brown and Amadon (1968) report the nests as hard to locate. Nests were similar in structure and construction materials to those of other studies. Nests composed entirely of broomweed are reported from Texas (Bent 1938), although most authors described the nest as simply a bulky structure of weeds and twigs (Brown and Amadon 1968, Oberholser 1974, Layne 1978).

In central Texas, two-thirds of 35 nests observed were reoccupied annually, but whether by former owners was not known (Schultze 1904). In this study, four of six nests had been previously used by caracaras. Farquhar (1986) reported caracaras using White-tailed Hawk (*Buteo albicaudatus*) nests on the APCNWR, and Mader (1981) noted one caracara nest refurbishment in Venezuela.

We suspect eggs laid in June were second broods from Pairs 1 and 5, based on our confidence at identifying the adults from daily behavior observations. Howell (in Bent 1938) reported one case of double brooding, but whether by the same parents was unknown. Doubling brooding has never been confirmed, although it was suspected (Slud 1964, Palmer 1988).

We observed copulations throughout the breeding season, which may help to maintain the pair bond (Newton 1979). Eggs were smaller than those reported by Bent (1938) and Oberholser (1974) and weighed less than those reported by Newton (1979). We found most nests had a clutch size of two, unlike Bent (1938) who reports a larger percentage of clutch sizes of three. The lengths of incubation and nestling periods were similar to those of earlier studies (Bent 1938, Layne 1978, Newton 1979).

Timing of nest initiation at our study was comparable to those of other studies. Four nests in Arizona had nestlings in May (Levy 1961, Ellis et al. 1988), and one nest in Texas had young in July (Ellis et al. 1988). Layne (1978) reported that the young fledge at about eight weeks.

Rivera-Rodriquez and Rodriquez-Estrella (1992) found 83% of 16 caracara nests in Mexico in 1990 were successful. They did not define nesting success using the Mayfield method. In this study, lower nest success for the incubation and nestling periods was the result of failure of Nest 2 and nestlings preyed upon by red imported fire ants in the second nesting attempt by Pairs 1 and 5.

Our data provides insight into length of the post-fledging dependency period, which was previously unknown (Newton 1979). Dillon (1961) last saw a family group in Central Texas in late June or July and did not see the nesting pair again until the following January. The duration of the post-fledging dependency period may be longer than reported here, as we had a narrow definition of this period and we did not use radio-transmitters to monitor fledglings.

ACKNOWLEDGMENTS

We gratefully acknowledge the assistance and cooperation of personnel at the APCNWR and numerous volunteers including J. Strater, R. Hicks, J. Weltzin, D. Carrie, R. Carrie, R. Benson, R. Duran, R. Engelbrecht, K. Northrup, C. and K. Hendry, J. Johnston, J. Holtkamp, and J. Kent. We also thank O. and M. Benton, D. and L. Underwood, and R. Kaechele for providing access to their land. We thank J. Morrison, D. Carrie, and two anonymous reviewers for their helpful comments on the manuscript. We thank the APCNWR for providing housing and transportation. This study was funded by grants from the Feliciana Corporation, International Research Expeditions, and the Texas Ornithological Society.

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Wilson Bull., 108(3), 1996, pp. 524–534

BREEDING BIOLOGY OF THE JABIRU IN THE SOUTHERN LLANOS OF VENEZUELA

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Abstract.—I studied the breeding biology of the Jabiru (*Jabiru mycteria*) at Hato El Frío (state of Apure, Venezuela) during two breeding seasons. I located 22 nests during 1989–90 and 28 in 1990–91. Jabiru nests were 8–26 m from the ground in ten different species of trees, with *Sterculia apetala* the most commonly used (36.4% of the nests). Storks laid eggs between August and November. The greatest number of clutches were in September. Average clutch size was 3.4 eggs (range: 2–5; N = 17), with four eggs the most frequent clutch size. Fledglings left their nests in January or February at the age of 12–13 weeks but were still dependent of their parents for a period of up to two months. Nest success was 47.0% in 1989–90 and 47.6% in 1990–91; productivity (fledglings/active nest) was 0.94 and 1.00 respectively. In 1990–91, only 20% of eggs produced fledglings. Most nests (75%) failed during incubation. Main causes of nest failure were abandonment, nests falling, and predation by Crested Caracaras (*Polyborus plancus*). *Received 20 Aug. 1995, accepted 15 Jan. 1996.*

The Jabiru (*Jabiru mycteria*) breeds east of the Andes from southern Mexico to northern Argentina (Blake 1977, Hancock et al. 1992). Despite its large size and wide distribution, the breeding biology of this stork is poorly known (Kahl 1971, Luthin 1987, Hancock et al. 1992). Kahl (1971, 1973) and Spaans (1975) reported on the status, behavior, and reproduction of the species in Argentina and Surinam. Thomas (1981) described nesting of the Jabiru in the central llanos of Venezuela (state of Guárico) and made a behavioral comparison of the species of storks that coexist in the region (Thomas 1985).

The Jabiru appears to be widespread but not abundant in the llanos of Venezuela (Ramo and Busto 1984, Ogden and Thomas 1985). I found no literature reports on the recent status of the species in this region. Conservation of the Jabiru in the llanos is threatened by continuous loss of forests and foraging sites, the massive use of pesticides in agricultural lands, and the proliferation of artificial dikes for water management (Ayarzagüena et al. 1981, Luthin 1987, Morales 1990, González 1993). Luthin (1987) strongly suggested that research on the ecology and status of the Jabiru should be undertaken on each distinct population in order to develop a global conservation stratregy for the species.

STUDY AREA AND METHODS

I studied Jabirus at Hato El Frío, a 78,000-ha private cattle ranch located in the southern or flooded plains of Venezuela, betwecn the villages of El Samán and Mantecal (7°35′–

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7°55′N, 68°50′–69°00′W) in the state of Apure. The study area is a tropical wet savanna with a highly seasonal distribution of rainfall. Mean annual rainfall is 1653 mm (period: 1969–1988), with more than 80% falling between May and October (rainy season), when much of the land is flooded up to one meter. Rainfall is very scarce between November and April (dry season), when much of the land becomes dry and water is restricted to a few streams, lagoons, and deepest marshes. The climate is tropical and mean monthly temperature is more or less uniform throughout the year, ranging from 28.6°C in March to 25.4°C in July.

Following Ramia's (1967) classification of llanos landscape types, the study area belongs to the group named "savannas of banco, bajío and estero". More than 80% of the land is occupied by herbaceous savanna vegetation, while the rest is covered by gallery forests and small isolated forested islands locally called matas. A detailed description of vegetation communities present at Hato El Frío can be found in Castroviejo and López (1985).

The study area was surveyed daily along fixed ground routes between July and September in 1989 and 1990, for pairs of Jabirus and for nesting attempts. In 1990, a fixed-wing aircraft was also used to search for new nests. Nesting attempts were mapped. The status of every nesting attempt was then monitored weekly until the nest was abandoned by adults or until fledglings made their first flight. A mirror on an extendable pole (also used to estimate nest height) was used to observe the contents of lower nests, but in most cases it was necessary to climb the tree or to use a ladder to reach nest level. Many of the nests were inaccessible from the ground, and their status in 1989–1990 was determined by prolonged observation of the birds' behavior. During 1990–1991, a fixed-wing aircraft was used to check the contents of inaccessible nests. The sexes were distinguished by body size and length and curvature of bill (Kahl 1971), later confirmed by copulation position.

Repeated visits to wading bird nests can severely bias the reproductive parameters studied (Tremblay and Ellison 1979, Frederick and Collopy 1989b, Kushlan 1992). On each visit, the distance at which adults left the nest in response to human approach, the total time spent near each nest and the length of time it took the birds to return to the nest were recorded. Careful observations were made for possible predation attempts while in the vicinity of the nest. To minimize disturbance, nests containing chicks more than two weeks old were not climbed; after this stage, chicks were easily visible using 12× binoculars or a 20× telescope, but eight visits to nests with older chicks were made to collect regurgitation samples (González 1993). No nests were climbed more than three times during incubation and the first two weeks after hatching. In every case, I avoided stormy or rainy days and direct sunshine to prevent thermal stress to nest contents (Dusi and Dusi 1978, King 1978).

Nesting attempts were categorized as having nest construction activities and permanent occupation by a pair of Jabirus. Active nests were those in which at least one egg was laid or, in inaccessible nests, those in which continuous incubation activity by adults was observed. Successful nests were those in which at least one chick fledged, and unsuccessful nests those that lost all eggs or chicks.

RESULTS

Breeding dates.—The Jabiru nesting period in the southern llanos began in the latter part of the rainy season and extended to the middle of the dry season. Laying was from mid-August to mid-November, with the greatest number of clutches laid in September (66.6% in 1989 and 50% in 1990, Fig. 1). The nesting season began later in 1989 than in 1990; in

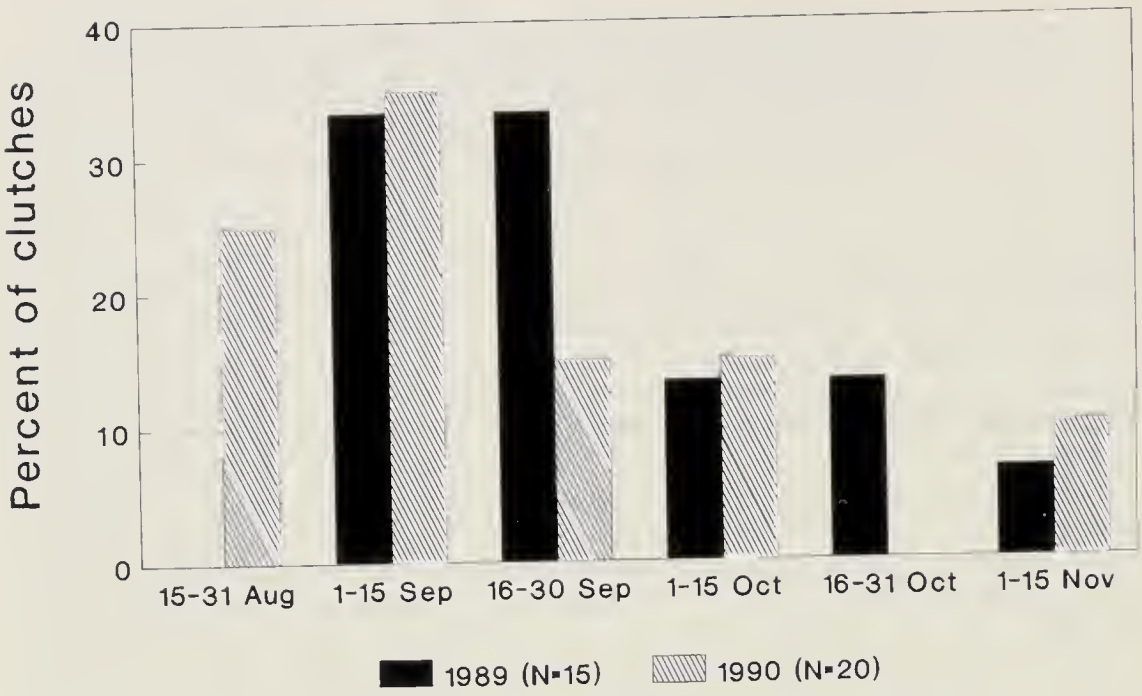

FIG. 1. Jabiru laying dates at Hato el Frío in 1989 and 1990.

the first season, no eggs were laid until September, while in 1990, 25% of the clutches were initiated in the second half of August (Fig. 1).

Nestlings stayed in the nest for about three months (84–93 days; N = 3 nests). Most of the 1989 successful nestlings made their first flight from 1 to 20 January 1990 (64.3%); the remaining ones fledged in February (Fig. 2). After their first flight siblings stayed together and were fed by their parents in nearby wetlands for a period of 6–8 weeks (González 1993). Therefore, successful Jabiru pairs were involved in reproductive tasks for almost seven months a year (Fig. 2).

Nest site.—Most of the nests (78.1%) were in small isolated forested islands (matas) of 0.2–2 ha, 3.1% were in matas of more than 50 ha, 9.4% were in gallery forests and the remaining 9.4% were in solitary trees. Almost all the Jabiru nests were solitary and owners defended a breeding territory of 300–500 m around their nests by chasing other Jabirus and other wading bird species that flew or foraged in that area. Mean distance to nearest conspecific nest was 1.9 km (range: 1.2–2.8). Three nests were built in the center of mixed-species colonies containing other wading birds such as White-necked Herons (*Ardea cocoi*), Great Egrets (*Casmerodius albus*), and Maguari Storks (*Ciconia maguari*).

Nests generally were built at the top of one of ten different species of large broad-leaved trees. *Sterculia apetala* was the most frequently used (36.4% of the nests), followed by *Ficus* sp. (18.2%) and *Pithecellobium saman* (9.1%). Other trees that supported Jabiru nests were *Spondias*

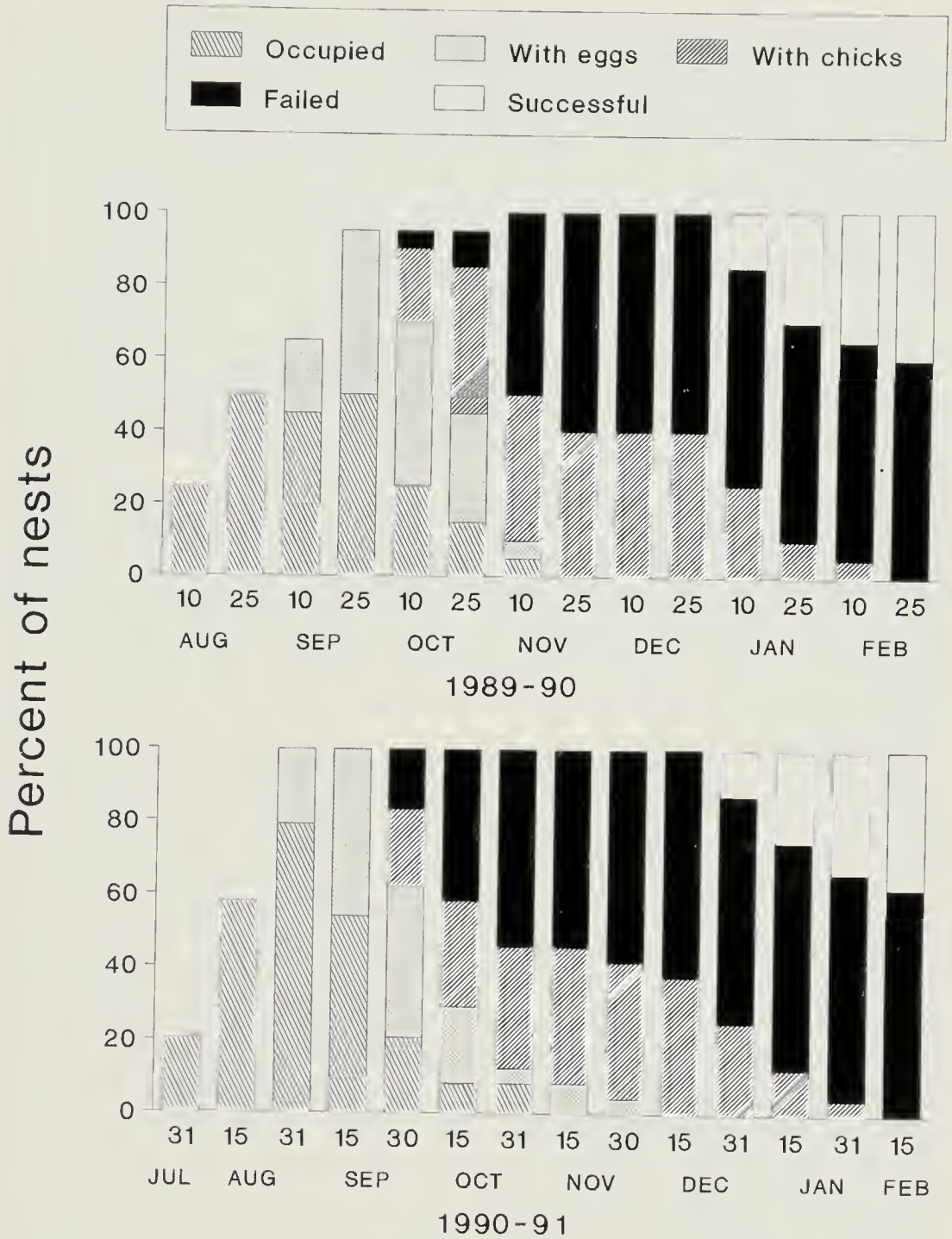

FIG. 2. Phenology of the 1989–90 (N = 20 nests) and 1990–91 (N = 24 nests) breeding seasons.

mombin, Acrocomia sclerocarpa, Ceiba pentandra, Tabebuia sp., *Sapium biglandulosum, Vitex* sp., and *Coccoloba caracasana.*

The average height of Jabiru nests on Hato El Frío was 15.4 m (range: 8–26). At a nearby ranch (Hato El Cedral), a nest was built less than 7

m from the ground. In nests located in dense forests (matas or gallery forests), the pair usually chose the highest tree around with an excellent view of the surrounding country. Nests were placed on forks of large limbs, between a large horizontal limb and the main trunk, or more usually in places where 3–4 branches crossed. Of the studied nests, 71.9% were on the top of the tree (crown branches), while the remaining 28.1% were on bifurcations of the trunk of a dead tree. All of the nests were less than 500 m from a large temporary or permanent wetland. Many of the nests (28.1%) were completely surrounded by deep marshes inundated during the nesting season, 21.9% were close to large permanent lagoons, and the remaining 50% were on the edge of a river or stream. These flooded wetlands were used by fledglings for 6–8 weeks after leaving the nest.

Construction and structure of nests.—All but two of 22 nests occupied in the 1989–1990 breeding season were reused in 1990–1991. 80% of those nests included part of their basic structure from one year to the next. The remaining 20% completely disappeared during the non-breeding season due to weather, broken supporting limbs, or the piracy of nest materials by other wading birds (in nests located in mixed-species colonies).

The time spent by Jabirus on nest construction before egg-laying depended on the previous state of the nest. Two nests were completely built in less than 20 days from a residual group of sticks remaining from the previous nesting season. Another nest, that kept its structure almost intact, was repaired in less than a week. The longest time it took a pair of Jabirus to build their new nest was seven weeks. Both sexes collaborate in nest construction or repairing, although sticks are mainly gathered by the male (Kahl 1971, Shannon 1987), at least in early stages of nest-building. In four nests monitored during an entire day, 66% of the new sticks for nest construction were gathered by the male and 34% by the female. In another nest that was apparently finished, all of the sticks and green materials were gathered by the male while the female remained on a nearby branch; only sometimes (30.7%), when the male came back with new materials, she jumped to the nest to position the sticks and then copulate. After egg-laying the female assumes a more equal role in nest-maintenance, as is the case in other storks (Kahl 1971).

Jabiru nests are oval to circular structures composed of sticks up to 160 cm long and 3.5 cm thick, with a central area lined with green plant material (grass, leaves and aquatic vegetation). Five nests measured during incubation averaged 205 × 180 cm (range: 180 × 130–220 × 180), with a central lined area of 100 × 85 cm (range: 80 × 70–120 × 90).

Nest thickness ranged between 40 and 60 cm, although one exceptional nest was 110 cm thick.

The gathering of sticks and green lining material continued without interruption throughout the nesting season, even in nests containing nestlings more than 80 days old and almost ready to fly. Initial size of nests changed significantly between incubation and fledgling stages. One nest was 220 × 170 cm during the incubation period and reached 270 × 190 cm two months later; the lined area also increased from 120 × 90 to 170 × 130 cm.

Clutch size and eggs.—Three complete clutches in 1989–1990 and 14 in 1990–1991 were counted. Grouping nests of both breeding seasons, average clutch size was 3.4 eggs (range: 2–5; N = 17), with six nests of four eggs and five nests of two eggs. A possible replacement clutch was found. The owners of this nest lost their original clutch of two eggs in the first week of October 1990, and the same pair was seen incubating during several consecutive days in the middle of November. The nest was abandoned during the first days of December before I could corroborate the existence of a replacement clutch and its size.

The eggs of the Jabiru are ovate to subelliptical. Coloration is white but becomes dirty with the passage of time. Six eggs from three nests, measured early in incubation, averaged 70.4 × 53.6 mm (length: 67.6–72.9; width: 49.8–55.9), with a mean weight of 110 g (range: 90–120).

Nesting success.—Of the 22 nesting attempts during the 1989–1990 breeding season, five were abandoned before egg-laying or any incubation activity by Jabirus. Three of these failed attempts were abandoned in an early stage of nest construction, while the other two nests were apparently finished and many copulations occurred in them before they were abandoned. Territorial pairs of abandoned nests remained in the area for up to two months, usually perching on the same tree that supported the nest. It is unlikely that pairs that failed during early stages of construction try to nest again in another area distant from the original one. Eight of 17 active nests during 1989–1990 fledged at least one chick (Table 1). The total number of fledglings produced in the study area was 16, with an average of 0.94 young per active nest. Nine nests (53%) failed, seven during incubation and two when they contained young chicks. Three nests fell from trees. Another had two infertile eggs that finally were abandoned. In the remaining five nests the cause of reproductive failure could not be determined. Partial losses were recorded in the eight successful nests. One egg from a clutch of three was infertile but remained in the nest for more than a week after the hatching of the other two. In two nests with initial brood size of three, the two youngest chicks were considerably smaller than their sibling and died during the first month of life,

TABLE 1

REPRODUCTIVE SUCCESS OF THE JABIRU ON HATO EL FRÍO DURING THE BREEDING SEASONS OF 1989–90 AND 1990–91

Nest variable	1989–90	1990–91
Occupied nests	22	28
Active nests[a]	17	21
Successful nests	8	10
% of nests successful[b]	47.0	47.6
Number of fledglings	16	21
Fledglings/active nest	0.94	1.00
Fledglings/successful nest	2.0	2.1

[a] Producing a clutch of eggs.
[b] Producing at least one chick to fledging age.

probably due to starvation. At another nest, one of three nestlings 65–70 days old died during a premature first flight or a fall during flapping exercises.

In the breeding season of 1990–1991 21 of 28 nesting attempts resulted in active nests. Ten were successful (47.6%). The total number of fledglings produced in the area was 21 (Table 1). Using data from 14 closely monitored nests, I estimated that only 20% of the eggs laid produced fledglings. Eight nests failed during incubation and three after hatching. One nest with two nestlings 3–4 weeks old fell when the supporting limb broke. In three failed nests, I observed Crested Caracaras (*Polyborus plancus*) eating eggs (2 nests) and nestlings 9–14 days old (1 nest); chicks and eggs were completely consumed at the nest. It is unknown whether this was predation or post-abandonment scavenging (see Frederick and Collopy 1989c). In one of these nests several days before predation, the pair of Jabirus left the eggs alone for long periods of time, which suggests that abandonment might have been the actual cause of failure. Brood reductions occurred in three successful nests, which lost a total of four nestlings. In two nests with initial brood size of three, the youngest chick died apparently of starvation; in another nest, with initial brood size of four, two chicks died during the first month of life.

DISCUSSION

Jabirus begin breeding in the southern llanos of Venezuela in August and some breeding occurs until February of the following year. Egg-laying takes place mainly during September, and most fledglings leave their nests in January. The dates of egg laying coincide with the period of major flooding, when adult Jabirus can easily find abundant food in

inundated marshes, mainly freshwater eels (Kushlan et al. 1985, Thomas 1985, González 1993). Fledglings make their first flight in the middle of the llanos dry season, when the absence of rains and rapid drying result in large concentrations of fishes in the few lagoons and ponds that still preserve some water (González 1993). The begining of the breeding season, as well as nesting success of the Jabiru in the southern llanos, may be related to the onset and quantity of rainfall and the effect they have on water level and food availability. This is similar to other wading bird species that breed in wetland habitats distinguished by a marked seasonal fluctuation in water level (Ogden et al. 1980, Ayarzagüena et al. 1981, Frederick and Collopy 1989a). Breeding dates in the study area are similar to those reported in literature for Jabirus in other regions. Kahl (1971) reported that the egg-laying period extends from July to October in Argentina and Brasil. Spaans (1975) recorded egg laying during August and September in Surinam. Laying dates in Guyana, Brazil, and Colombia are also between July and October (in Kahl 1971). In the central llanos of Venezuela, most of the clutches are laid during September and October (Thomas 1985).

The majority of the nests found in the study area were located in forested islands (matas) of less than 2 ha, with nests most frequently placed in *Sterculia apetala.* Other Jabiru nests reported from the llanos include 11 nests in the palm *Copernicia tectorum* (Thomas 1981) and two nests in *Pithecellobium saman* (Ogden and Thomas 1985). Spaans (1975) mentioned one nest in *Ceiba pentandra* in Surinam and Kahl (1971) reported six nests in palms and other medium-size trees in Argentina. In general, Jabirus build nests far from other wading bird nests. However, three nests in the study area were in the center of mixed-species colonies. Naumburg (in Kahl 1971) also reported one Jabiru nest in a large colony of Wood Storks (*Mycteria americana*) in Brazil.

Average clutch size in the study area was 3.4 eggs. Most completed clutches were comprised of four eggs. Three clutches (17.6%) were comprised of five eggs, a number that is considered rare for Jabirus (Kahl 1971, Hancock et al. 1992). Hagmann (in Bent 1926) reported clutches of two and three eggs in Jabiru nests, while Lloyd (in Bent 1926) reported that four eggs was the most frequent clutch size in this species. Kahl (1971) reported two clutches of four eggs in Argentina. The average size of six eggs was slightly lower than average size reported by Bent (1926): 73.4 × 58.2 mm (N = 8).

Jabirus exhibit territoriality throughout the nesting season (Kahl 1973, Thomas 1985, Shannon 1987). As a consequence of this agressive behavior, Thomas (1981) suggests that it is unlikely that more than one female could lay eggs in the same nest. Although I absolutely agree with

these statements, however, an exceptional event took place in one of the studied nests: for more than three hours in the morning of 3 October 1989, a male copulated repeatedly with two different females, each of which took turns in the nest; finally, one of the females was expelled by the other and left the area. The nest was abandoned three weeks after this event and no incubation activity was observed during that period.

Nest success in the study area was 47% in 1989–1990 (N = 17 nests) and 47.6% in 1990–1991 (N = 21 nests), with only 20% of the eggs producing fledglings (N = 14 nests). There are no other published data on nesting success of this species in other geographical areas to compare with my results.

Most of the unsuccessful nests failed in an early stage of incubation. The abandonment of the nest by adults and predation upon eggs or nestlings seem to be the two most important causes of nesting failure in the studied population; it is very difficult to determine which of them occurs first (Frederick and Collopy 1989c). The Crested Caracara, an abundant raptor in the southern llanos, was the main predator of eggs and nestlings of Jabirus and, in general, of all wading birds in the study area (González 1993).

Of 22 nests recorded during the 1989–1990 breeding season, 19 were reused in 1990–1991 (86.4%). Thomas (1981) reported that in the central llanos of Venezuela, new nests were made every breeding season because palms supporting nests died after the first year. In the study area I found only one nest in a palm in 1989–1990; this nest fell during the incubation period and was not reused in 1990–1991.

Of the 17 active nests monitored in the first breeding season, only eight were again active during the second one. Considering the successful nests of 1989–1990 (N = 8), only three of them were active in 1990–1991, and only two were again successful. If we assume the hypothesis that Jabiru pairs remain mated in successive seasons and use the same nesting site, which is supported by several observations on their nesting behavior and territoriality (Kahl 1973, Thomas 1985, González 1993), my data would indicate that less than half of active pairs in one season are also active during the following one and that only 25% of successful pairs are successful in a second consecutive season. This may be due to a mere coincidence or could suggest that Jabirus have some trouble breeding successfully in consecutive years, perhaps due to the great amount of time that adults spend on breeding-related activities (6–7 months). Long-term studies in the same area that include monitoring of marked birds are needed to assess these statements.

ACKNOWLEDGMENTS

I thank J. Castroviejo for his encouragement during this work. I also thank all the Maldonado family, owners of Hato El Frío, for their hospitality and for giving us all the facilities

to develop our work. I am grateful to F. Ibáñez, V. Rosales, P. Quiñones, and the staff of Estación Biológica El Frío for their assistance during the field work. I am also very grateful to P. Frederick, C. Ramo, E. de Juana, B. T. Thomas, and C. R. Blem for reviewing earlier drafts of the manuscript. Financial support was provided by grants of Asociación de Amigos de Doñana and Universidad Complutense de Madrid.

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Wilson Bull., 108(3), 1996, pp. 535–539

EFFECT OF EGG SIZE ON PREDATION BY WHITE-FOOTED MICE

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Abstract.—We compared predation by wild-trapped, caged white-footed mice (*Peromyscus leucopus*) on eggs of Japanese Quail (*Coturnix coturnix*) and Zebra Finches (*Poephila guttata*) to test the effect of egg size. Nine male and nine female mice were weighed, acclimated to cages for 24 h, and presented with two wicker nests, one containing a Japanese Quail egg (33 × 23 mm) and the other a Zebra Finch egg (16 × 12 mm). Nests were checked at 2, 4, 6, 8, 12, 16, and 24 h; after 24 h, no quail eggs were depredated, but 16 of 18 finch eggs were destroyed. Given their ability to consume small eggs and their ubiquity and abundance, white-footed mice are potentially significant nest predators. *Received 21 Nov. 1995, accepted 15 Feb. 1996.*

While evaluating the effect of forest understory density on predation of artificial nests, we found that white-footed mice (*Peromyscus leucopus*) frequently were recorded by remotely-triggered cameras at ground and shrub nests containing eggs of Japanese Quail (*Coturnix coturnix*). Many of these same nests appeared to be undisturbed at the end of the exposure period (DeGraaf et al., unpubl. data). Eggs of *Coturnix* commonly are used to simulate those of passerines in studies of nest predation because they are the smallest eggs commercially available in large quantity. Many studies have recently been conducted using *Coturnix* eggs to assess effects of habitat fragmentation or structure on forest birds, especially Neotropical migrants (e.g., Small and Hunter 1988, Wilcove 1985, Martin 1987), but none of these studies tested whether mice can open songbird eggs but not the larger quail eggs. Maxson and Oring (1978) reported that predation on Spotted Sandpiper (*Actitis macularia*) eggs essentially was eliminated after *Peromyscus* were trapped out of the study area, indirectly implicating mice as nest predators. White-footed mice have been documented as predators on nests of Prothonotary Warblers (*Protonotaria citrea*) (Guillory 1987). Do *Coturnix* eggs allow assessment of the role of mice as predators on artificial nests?

We compared predation by caged white-footed mice on eggs of Japanese Quail and Zebra Finches (*Poephila guttata*) to test the effect of egg size. *Coturnix* eggs averaged approximately 33 × 23 mm, and finch eggs were approximately 16 × 12 mm. For comparison, egg sizes of several forest passerines are: Gray Catbird (*Dumetella carolinensis*), 26 × 19

USDA Forest Service, Northeastern Forest Experiment Station, Univ. of Massachusetts, Amherst, Massachusetts 01003.

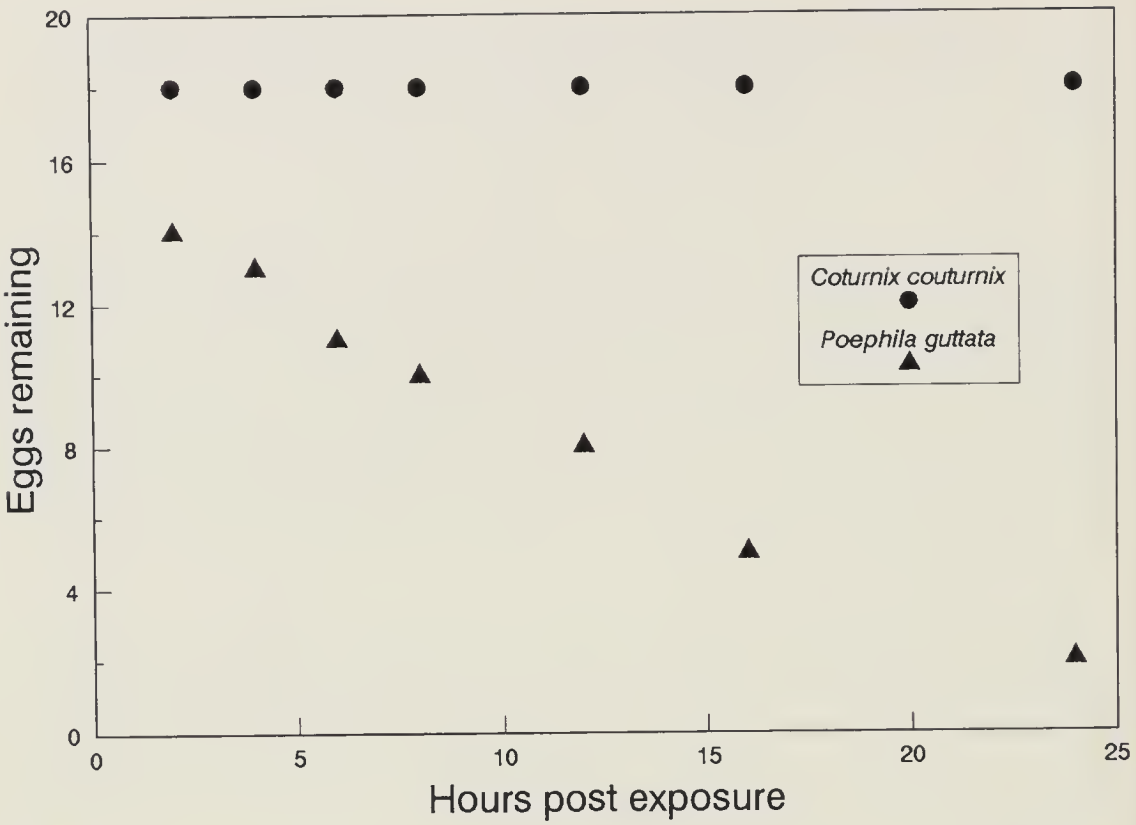

FIG. 1. Numbers of large Japanese Quail (*Coturnix coturnix*) and small Zebra Finch (*Poephila guttata*) eggs remaining after one egg of each type was simultaneously exposed to 18 wild-trapped white-footed mice (*Peromyscus leucopus*) for 24 h.

mm; Wood Thrush (*Hylocichla mustelina*): 25 × 19 mm, and Black-and-White Warbler (*Mniotilta varia*): 17 × 13 mm (Harrison 1975).

METHODS

Eighteen white-footed mice, nine males and nine non-lactating females, were selected randomly from 25 individually caged mice wild-trapped over a two-day period in western Massachusetts. Mice were weighed, sexed, and acclimated for at least 24 h to cages in a large, unheated vacant barn. Cages were provided with wood-chip litter, water, and food ad lib. Weights of mice ranged from 11.7 to 27.4 g, representing juvenile, subadult, and adult stages. Mean weight for both males and females was 20.3 g. Each mouse was then provided with two aviculturists' wicker nests, one containing a Zebra Finch egg and the other a Japanese Quail egg, at 09:00 on 13 October 1995. Nests were checked at 2, 4, 6, 8, 12, 16, and 24 h post-exposure and predation on eggs was recorded.

RESULTS

After 24 h exposure, no *Coturnix* eggs were depredated, but 16 of 18 finch eggs were destroyed (Fig. 1). White-footed mice are primarily nocturnal (Baumgardner et al. 1980), but predation on finch eggs commenced shortly after exposure, i.e., in mid- to late morning. Mean times until depredation differed ($0.05 > |t| > 0.02$) for female ($\bar{x}$ = 6.5 h) and male ($\bar{x}$ = 15.5 h) mice. We detected no relationship between mouse weight and time to egg depredation. The two finch eggs not eaten within 24 h were given to two other randomly

chosen mice to determine whether these eggs were unpalatable; both eggs were eaten within 24 h. All but one finch egg were opened from the side and the contents eaten through the resulting hole; one egg was opened at both ends. No *Coturnix* eggs were broken after exposure for 13 days.

DISCUSSION

White-footed mice probably are significant predators of passerine eggs, but based on the results of our experiments, their effect cannot be experimentally measured using *Coturnix* eggs. The inability of mice to consume quail eggs may be due to several factors. First, the jaw-gape of mice may be too small. We measured the jaw-gape of 22 previously-frozen, locally wild-trapped adult white-footed mice. The jaws were opened, using loops of fine wire until resistance was felt, and the distance between upper and lower incisor tips measured. Jaw-gape ranged from 7.0 to 10.5 mm, with a mean of 8.9 ± 1.1 mm. Such a gape seems too small to open *Coturnix* eggs, which were 23 mm in smaller diameter. Also, eastern chipmunks (*Tamias striatus*) did not open *Coturnix* eggs even though they had previously consumed the contents when presented with broken eggs (Haskell, 1995a).

Second, eggs from commercial quail farms may have thick shells due to diet supplements; this was the case with our quail eggs. Shell thickness may partly explain why *Coturnix* eggs were not opened by mice in the present study, but Spotted Sandpiper eggs, which are about the same size—32 × 23 mm (Harrison 1975:69)—apparently were depredated by mice in Maxson and Oring's (1978) study. We measured shell thickness of five fragments of each of two Spotted Sandpiper eggs, one from the Carnegie Museum and another from the University of Massachusetts Museum of Zoology; both measured 102 microns thick. Two Japanese Quail eggs similarly measured were 229 and 216 microns thick. Japanese Quail egg shells were more than twice as thick as Spotted Sandpiper eggs.

Third, egg shape may be a factor. Spotted Sandpiper eggs are oval to pyriform (Harrison 1975:69); *Coturnix* eggs are short-oval. Mice may be able to open the small end of pyriform eggs that are the same size as short-oval eggs. The eggs of most forest songbirds in the Northeast are oval or short-oval, rarely long-oval (Harrison 1975).

Coturnix eggs and those of domestic chickens may be useful to assess predation on eggs of waterfowl and upland game birds, but such eggs are too large or too thick-shelled to adequately assess predation on those of smaller passerines. For example, Ovenbird (*Seiurus aurocapillus*) eggs average 20.2 × 15.5 mm; those of Chestnut-sided Warbler (*Dendroica pensylvanica*) average 16.7 × 12.4 mm (Bent 1953). Haskell (1995a) has shown that the jaw-gape of chipmunks was large enough to break the

eggs of most Neotropical migrant passerines that nest in forest or scrub, but was too small to break Japanese Quail eggs.

The appearance and positioning of artificial nests can be made to approximate those of breeding birds (e.g., Martin 1987, Yahner and Voytko 1989) and precautions taken to avoid leaving human scent at artificial nests (e.g., Whelan et al. 1994). But, if the eggs used cannot be broken by the full suite of potential predators in the habitats being studied, total predation rates or effects of habitat differences cannot be estimated. For example, if the relative abundance of predator species varies across habitat fragment sizes, the bias inherent in using too-large eggs can lead to spurious correlations between fragment size and predation rate. In an investigation of whether the rate of nest predation by small-mouthed mammalian predators varied by fragment size, Haskell (1995b) found that the number of eggs preyed upon by such predators increased with fragment size; in large fragments the predominant nest predators were those which quail egg experiments failed to sample. In both North America (Yahner and Scott 1988) and Europe (Andrén 1992), nest predators in small fragments tend to be large mammals, e.g., raccoon, (*Procyon lotor*) or corvids. Small mammals, e.g., white-footed mice, in contrast, are ubiquitous and abundant, inhabiting many habitat types (Lackey et al. 1985) and a wide range of forest successional stages within extensive forests (Healy and Brooks 1988). Reitsma et al. (1990) suggest that *Peromyscus* may be more important as nest predators than previously thought.

The presence of mice at artificial nests, their demonstrated ability to consume small eggs, and their ubiquity and abundance render them potentially significant nest predators. Eggs susceptible to mouse depredation must be used to estimate their impact. We suggest that such eggs be used in future field studies that use artificial nests to validate mouse predation on nests of small forest passerines.

ACKNOWLEDGMENTS

We thank W. R. Danielson for providing Zebra Finch eggs, W. M. Healy for help trapping mice, R. Panza and K. Doyle for providing samples of Spotted Sandpiper eggs, and R. A. Askins, D. G. Haskell, R. T. Holmes, and W. M. VanderHaegen for their critical reviews. M. A. Sheremeta typed the manuscript, and R. T. Brooks prepared the figure.

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Wilson Bull., 108(3), 1996, pp. 540–549

CAN CHECKLIST PROGRAMS BE USED TO MONITOR POPULATIONS OF BIRDS RECORDED DURING THE MIGRATION SEASON?

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ABSTRACT.—Quebec's ÉPOQ program compiles birders' "checklists," each of which reports numbers of birds seen on one day at one site. We analyzed ÉPOQ data from the migration season alone (1971–92), to see if these unstandardized counts might monitor trends in populations that nest farther north. Two sets of trends were computed for each of 58 species, from annual indices based either on abundance or on frequency of detection. Both spring ÉPOQ trends were significantly correlated with Breeding Bird Survey trends for Quebec, while only those based on abundance performed well in fall. There was a positive bias in magnitude of ÉPOQ trends, but negative ÉPOQ trends were reliable indicators of negative BBS trends. Analysis of sub-sets of the data showed that sample size had little qualitative effect. Checklist data should not be relied on for quantitative population monitoring, but they do contain useful information for detection or corroboration of negative trends. *Received 27 Aug. 1995, accepted 22 Jan. 1996.*

Most songbirds that breed in North America are monitored by the Breeding Bird Survey (BBS), a breeding season roadside survey along randomly chosen routes across the continent (Peterjohn 1994). Certain species are poorly covered by BBS, however, either because they nest too sparsely or locally to be covered by an adequate number of routes (many raptors and colonial birds, for example) or because they breed in remote areas where BBS routes are largely lacking (e.g., many northern boreal forest breeders). Counting of birds during their migratory passage has been suggested as a means of monitoring some of the species missed by BBS and as a means of corroborating trends detected by other programs. Relatively standardized daily counts of birds at bird observatories and hawk look-outs have been shown to document long-term trends in bird numbers similar to those reported by BBS (reviewed in Dunn and Hussell 1995).

Checklist compilation programs potentially offer another source of data on population trends of migrants. Checklists are pre-printed lists of species on which observers can record their observations for an area of any size and during a period of any length. Compilations of checklist data have several strong points: they cover broad areas where other data might be lacking, and they harness the energy of the myriad birders who already keep careful records of what they see. On the negative side, there is a

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great deal of "noise" in the data, because observations are made opportunistically at any site on any date without any limits on duration of observation or skill of observers. Birders may concentrate on "productive" locations, and likely are not distributed evenly in time (favoring weekends and peak migration periods). There is also potential for consistent bias over time; for example, as bird distribution and abundance change, birders may move to new locations and/or change their search strategies to keep their birding interesting. Moreover, steady improvement in birders' skills and optical aids may have increased detectability of certain species over the years.

Despite these features of checklist data that might obscure any changes in bird populations, it is possible that they still contain useful trend information. Cyr and Larivée (1993) looked for evidence of this, analyzing spring and fall data from the Étude des Populations d'Oiseaux du Québec (ÉPOQ). This is North America's longest-running and largest checklist compilation program, and data are collected according to guidelines designed to maximize scientific value of such projects (Dunn 1995). The ÉPOQ trends in Cyr and Larivée's (1993) study had the same sign (positive or negative) as BBS trends for Quebec in 62% of the 74 species analyzed. These results are not strong, but the analysis was of simple presence/absence data which are limited in ability to detect trends (Bart and Klosiewski 1989).

The aim of this paper is to examine more closely whether checklists might contain useful information on population trends and to determine whether further analyses would be worthwhile.

METHODS

ÉPOQ data are semi-standardized in that each record contains the number of birds seen or heard on a single day's visit to a single locality (within one minute of latitude and longitude, or roughly 3.2 km^2; Cyr and Larivée 1993, 1995). Most lists are submitted by experienced birders, and the vast majority come from the whole length of the St. Lawrence corridor in southern Quebec (map in Cyr and Larivée 1995). Data are quite well distributed over all possible dates (individual days within a year). Although there are fewer than 30 checklists for most dates (54% of spring dates, 89% of fall dates), there are only 29 dates in the 22-year analysis period with no checklists at all (0.2% of spring dates and 1.2% of fall dates), all in the early 1970s. The average number of lists per date increased from 4.5 to 25.4 over the study period. We analyzed all available data within the chosen date limits (see below) regardless of geographic location, length of daily birding trips, number of observers or weather conditions, but did take into account the seasonal pattern in numbers of birds seen, as described below.

We selected data from the spring and fall migration "windows" for each of 58 songbirds (Table 1) for the period 1971–92. This ensured that observations of breeding birds were not mixed with observations of migrants, as could occur if we used data from a single period covering the migration periods of all species. To determine these windows, average daily abundance was plotted against date for each species. Dates were then chosen that included

TABLE 1

SPECIES AND CODES FOR FIGURES, QUEBEC BBS TRENDS, AND ÉPOQ TRENDS (BASED ON ABUNDANCE, FULL DATA SET)[a]

Species	Code (for figures)	ÉPOQ trend		BBS trend
		Spring	Fall	
Chimney Swift (*Chaetura pelagica*)	a	−0.4	−1.8	−3.5
Ruby-throated Hummingbird (*Archilochus colubris*)	b	1.8*	1.7*	1.0
Northern Flicker (*Colaptes auratus*)	c	−0.7+	0.2	−2.1+
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	d	0.3	−0.6	−0.2
Great Crested Flycatcher (*Myiarchus crinitus*)	e	0.3	−0.5	−2.5
Eastern Wood-Pewee (*Contopus virens*)	f	−0.1	−1.0	−1.4
Eastern Phoebe (*Sayornis phoebe*)	g	0.1	2.0+	0.9
Least Flycatcher (*Empidonax minimus*)	h	0.6	−0.9	−2.3
Yellow-bellied Flycatcher (*E. flaviventris*)	i	1.4	−0.3	4.5
House Wren (*Troglodytes aedon*)	j	−0.8	0.5	−3.8+
Winter Wren (*T. troglodytes*)	k	0.7	2.3+	3.5
Golden-crowned Kinglet (*Regulus satrapa*)	l	1.2+	4.0*	−2.0
Wood Thrush (*Hylocichla mustelina*)	m	−1.3*	−4.9*	−3.5
Veery (*Catharus fuscescens*)	n	−0.0	−0.9	−0.1
Swainson's Thrush (*C. ustulatus*)	o	−0.0	−3.2*	−2.3
Hermit Thrush (*C. guttatus*)	p	0.6	−0.1	−0.7
American Robin (*Turdus migratorius*)	q	1.0	1.0	1.0
Gray Catbird (*Dumatella carolinensis*)	r	−2.2*	−1.6+	−5.5*
Brown Thrasher (*Toxostoma rufum*)	s	−2.4*	−2.6	−4.6*
Solitary Vireo (*Vireo solitarius*)	t	0.6	4.5*	8.6+
Red-eyed Vireo (*V. olivaceus*)	u	1.4*	2.0*	2.3*
Warbling Vireo (*V. gilvus*)	v	2.2*	1.9	1.7
Philadelphia Vireo (*V. philadelphicus*)	w	2.0*	−0.1	5.2
Tennessee Warbler (*Vermivora peregrina*)	x	0.5	−1.3	−4.7
Nashville Warbler (*V. ruficapilla*)	y	0.4	−1.9+	−4.2
Northern Parula (*Parula americana*)	z	0.4	3.7*	−0.3
Black-and-white Warbler (*Mniotilta varia*)	A	1.1+	2.0*	4.7+
Black-thrt. Blue Warbler (*Dendroica caerulescens*)	B	0.1	2.6*	1.3
Blackburnian Warbler (*D. fusca*)	C	0.5	4.5*	3.7
Chestnut-sided Warbler (*D. pensylvanica*)	D	0.5	1.8+	−6.5
Cape May Warbler (*D. tigrina*)	E	−1.3*	0.5	−0.2
Magnolia Warbler (*D. magnolia*)	F	1.3*	1.4	5.8
Yellow-rumped Warbler (*D. coronata*)	G	0.5	0.4	2.8+
Black-throated Green Warbler (*D. virens*)	H	0.6	2.0*	0.0
Bay-breasted Warbler (*D. castanea*)	I	−1.3+	−0.5	−9.0
Yellow Warbler (*D. petechia*)	J	0.8*	0.2	2.9+
Mourning Warbler (*Oporornis philadelphia*)	K	0.4	0.0	0.2
Canada Warbler (*Wilsonia canadensis*)	L	0.7	−0.4	−0.6
Ovenbird (*Seiurus aurocapillus*)	M	1.2*	−0.0	−0.4
Northern Waterthrush (*S. noveboracensis*)	N	1.4*	−0.7	−0.5
Common Yellowthroat (*Geothlypis trichas*)	O	0.4	0.2	−2.2+
American Redstart (*Setophaga ruticilla*)	P	1.2*	1.5*	−2.0

TABLE 1
CONTINUED

Species	Code (for figures)	ÉPOQ trend		BBS trend
		Spring	Fall	
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	Q	−0.2	−2.9*	−4.8*
Vesper Sparrow (*Pooecetes gramineus*)	R	−0.3	−1.0	−6.8*
Savannah Sparrow (*Passerculus sandwichensis*)	S	−0.8*	−0.6	−2.3*
Song Sparrow (*Melospiza melodia*)	T	−0.6	0.4	−0.2
Chipping Sparrow (*Spizella passerina*)	U	1.1*	2.0*	1.4
Dark-eyed Junco (*Junco hyemalis*)	V	1.3	1.9+	−3.7
White-throated Sparrow (*Zonotrichia albicollis*)	W	−0.6	−0.6	−1.9*
Lincoln's Sparrow (*Melospiza lincolnii*)	X	1.7*	1.6*	−4.0*
Swamp Sparrow (*M. georgiana*)	Y	0.3	1.1	−5.0
Bobolink (*Dolichonyx oryzivorus*)	Z	−1.8*	−1.2+	−6.2*
Eastern Meadowlark (*Sturnella magna*)	2	−1.5*		−5.3*
Red-winged Blackbird (*Agelaius phoeniceus*)	3	−3.5*		−3.5*
Brown-headed Cowbird (*Molothrus ater*)	4	−4.3*		−7.2*
Common Grackle (*Quiscalus quiscula*)	5	−0.0		0.0
Northern Oriole (*Icterus galbula*)	6	−0.4	−1.6	−2.1
Scarlet Tanager (*Piranga olivacea*)	7	−0.6	−1.7	−1.8

[a] Significance of trends (1971–92) shown by: + = $0.05 < P < 0.10$, * = $P < 0.05$.

the seasonal rise and fall of numbers except for about one week at each end of the season, thus excluding the transitions between migration and stable numbers of either breeding or wintering birds. Of the 58 species analyzed, migration windows for 50 had also been calculated for Long Point, Ontario (Hussell et al. 1992). Timing of peaks and early/late dates differed between the provinces, but the "windows" (which excluded extreme dates) were very similar in both data sets. For convenience, the Long Point dates were used when available. Fall migration windows in Quebec were not clearly definable from ÉPOQ data for Eastern Meadowlark, Red-winged Blackbird, Brown-headed Cowbird, and Common Grackle; (scientific names in Table 1) so these species were excluded from fall analyses.

We calculated annual indices of abundance for each season for each species, using a regression procedure that adjusted the daily total of a species according to date within the season (adapted from the method described in Hussell et al. 1992). If we had merely calculated mean daily count, results would be heavily influenced by numbers seen in peak migration periods and especially by records from "fall-outs" (when heavy migration is halted by a weather front). Instead our approach determines whether the average count for each date (a single day in a single year) is higher or lower than the long-term average count for that date. The resulting annual index of abundance, therefore, reflects the average degree of positive or negative deviation from the expected daily values across the *entire* season.

We did not attempt to correct the data for weather effects or uneven distribution of observers throughout the season or the province. Such factors introduce variability to annual indices, but our assumption was that they did not change systematically through time and, therefore, should not contribute to spurious trends in bird numbers. Those factors most likely to produce consistent bias over time—improvement of skills or change in birders' search behavior, see introduction—cannot in any case be mitigated by data selection or analysis procedures.

Analysis details were as follows. The dependent variable in the regression (run separately for each species for each season) was log (mean daily count + 1), where "daily count" was number of birds per hour in the field for a single checklist, and one was added to the mean to allow log transformation of zeros. Each case was weighted by the number of checklists used to calculate daily mean abundance. Use of "birds/hr" helps standardize values from field trips of different lengths. Log transformation addresses the assumptions of the regression procedure by changing multiplicative to additive effects and by bringing the distribution of daily counts closer to normality (raw counts are skewed).

Independent variables included first to sixth order terms for day (day = 0 for a day near the center of the species-specific migration window) and dummy variables for each year except for one reference year (e.g., Y89 = 1 if year is 1989, otherwise Y89 = 0). The date terms allowed modelling of a relatively complicated seasonal pattern without adding so many terms as to produce overfit. Annual abundance indices were calculated from the coefficients of the dummy variables for year that were estimated in the regression. The annual abundance index was the value of the adjusted mean for year plus one-half of the error variance of the regression (so that corrected estimates in the original scale represent the mean instead of the median; see references in Hussell et al. 1992) back-transformed to the original scale by exponentiating and subtracting one.

A second analysis, similar to the above, was used to calculate annual indices based on frequency (the daily proportion of checklists on which the species was reported present). The only differences were that the dependent variable in the regression was the square root of the arcsin-transformed daily proportion, with appropriate adjustment prior to transformation of proportions equal to 0 or 1 (Snedecor and Cochran 1967:327–328), and we did not add half the error of the variance prior to back-transformation. We refer to this as the "date-adjusted frequency" index.

Trends were calculated separately for spring and fall indices. Those based on abundance were calculated from weighted linear regression of the log of the annual indices on year. (There was no need to add a constant before transformation because annual indices were never equal to zero.) Trends based on frequency were calculated with weighted linear regression of the square root of arcsin-transformed annual indices. In all trend calculations, weights were proportional to the number of checklists contributed each season during the species-specific migration period.

The number of lists compiled by ÉPOQ has increased steadily over the period analyzed from about 2,000 to about 10,000 annually (Cyr and Larivée 1995). In an attempt to circumvent possible bias from this source, as well as to determine what sample size might be sufficient, we reran all procedures on data sets consisting of 1000, then 500, cases selected randomly from each season each year.

ÉPOQ trends were compared to trends from the Breeding Bird Survey (BBS) for Quebec for the same set of years. BBS is a standardized roadside survey in which volunteers make 50 3-min stops every 0.8 km along prescribed routes, recording all birds seen and heard (Peterjohn 1994). Geographical coverage of Quebec is roughly equivalent in BBS and ÉPOQ. BBS trends were calculated using the Canadian Wildlife Survey version of the route regression analysis method (Erskine et al. 1992). All species analyzed were present on at least 22 BBS routes in Quebec during the study period. (The recommended number for meaningful analysis is 15.)

RESULTS

Full data set.—ÉPOQ trends based on abundance indices, both in spring and fall, were significantly correlated with BBS trends (Table 2).

TABLE 2

SPEARMAN RANK CORRELATION COEFFICIENTS BETWEEN ÉPOQ AND BBS TRENDS FOR QUEBEC, 1971–1992[a]

Season	ÉPOQ indices calculated as:			
	Abundance (Birds/hr)	(N)	Date-adjusted frequency	(N)
		Full data set		
Spring	0.58***	(45,578)	0.51***	(66,821)
Fall	0.55***	(27,682)	0.48***	(39,842)
		1000 cases per season		
Spring	0.53***	(19,804)	0.38**	(21,864)
Fall	0.47***	(17,334)	0.32*	(20,253)
		500 cases per season		
Spring	0.50***	(10,728)	0.35**	(11,000)
Fall	0.43***	(10,536)	0.09	(10,959)

[a] See methods for definition of the two ÉPOQ trend calculations. 58 species in spring, 54 in fall. Significance of correlation (two-tailed tests): * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. Total sample size in parentheses.

However, scatter plots showed that correspondence between the programs was not entirely one-to-one (Figs. 1A and 1B); that is, points were not evenly distributed about the dashed line representing equality of trends. ÉPOQ produced markedly more positive trends than BBS in those species that BBS showed to be declining. Significance of trend in ÉPOQ did not reflect significance in BBS (Table 3), although trends that were significant in both programs agreed in sign in all cases but one.

ÉPOQ trends based on date-adjusted frequency indices were also significantly correlated with BBS trends in both seasons (Table 2). The magnitude of trends based on frequency cannot be compared directly to BBS magnitude because the scales differ (BBS trends are expressed as annual percent change in abundance; ÉPOQ trends are the annual change in arcsin transformed annual proportions of checklists with the species present). However, if the two programs monitor the same phenomena, then the directions of trends should agree. This was largely the case for trends based on date-adjusted frequency indices for spring (Fig. 2A, which has a similar pattern to the spring abundance trends in Fig. 1A). However, fall frequency trends based on ÉPOQ data were much more likely to be negative than were BBS trends (Fig. 2B) and were also more negative than ÉPOQ trends based on abundance (Fig. 1B). Significance of ÉPOQ trends based on frequency did not reflect significance in BBS (Table 3).

FIG. 1. Trends in ÉPOQ abundance indices for spring (Part A, top) and fall (Part B, bottom) plotted against BBS trends. Trends expressed as annual percent change in abundance. Dashed line shows one-to-one correspondence. See Table 1 for species codes.

Reduced data set.—When the data set was reduced, analyses gave qualitatively similar results to all those presented above. Correlation coefficients were reduced, however (Table 2), due to increased scatter in ÉPOQ trends.

TABLE 3

NUMBER OF SPECIES WITH SIGNIFICANT OR MARGINALLY SIGNIFICANT ($P < 0.1$) TRENDS IN QUEBEC BBS AND ÉPOQ (FULL DATA SET)

Trend significant in:	ÉPOQ abundance trend		ÉPOQ frequency trend	
	Spring	Fall	Spring	Fall
ÉPOQ only	12	15	15	15
Both ÉPOQ and BBS	11	7	14	9
BBS only	7	9	5	8

DISCUSSION

Comparison of analyses.—ÉPOQ indices based on abundance of birds gave the best correspondence to BBS, producing trends that showed the highest level of agreement in direction and magnitude in both seasons.

Bart and Klosiewski (1989) found that BBS trends based on frequency indices generally had the same sign as trends based on abundance (positive or negative), but the two types of trends did not compare well in magnitude. We had similarly expected that ÉPOQ trends based on frequency would not correspond as well to BBS trends as those based on abundance, but this was borne out only by fall results (compare Fig. 1B with Fig. 2B).

Evaluation of checklists in monitoring populations.—The primary uses made of checklist data do not include population monitoring but rather a wealth of other applications such as documentation of range, timing of occurrence in a given region, unusual appearances, and site-specific species composition. These applications do not depend on standard observation protocol and appropriate sampling framework, whereas population monitoring does if it is to be statistically defensible. Nonetheless, our results suggest that checklist data, even when uncorrected for likely sources of spurious variability, do contain information on population trends, albeit biased. (We assume for the purpose of this discussion that BBS is an accurate, unbiased indicator of trends, but of course we cannot be certain of this.)

The positive bias in ÉPOQ trends (Fig. 1) is just what we might expect of checklist data as a result of improving skills and optical aids (see Sauer et al. 1994) or as a result of shifts by birders to more productive birding spots as species decline in previously-favored sites. The positive bias of ÉPOQ trends means that they are less reliable indicators of magnitude than are BBS trends. Analysis procedures could be altered to reduce variation introduced to ÉPOQ indices by factors such as uneven temporal and geographic distribution of observers, but this would likely help only to

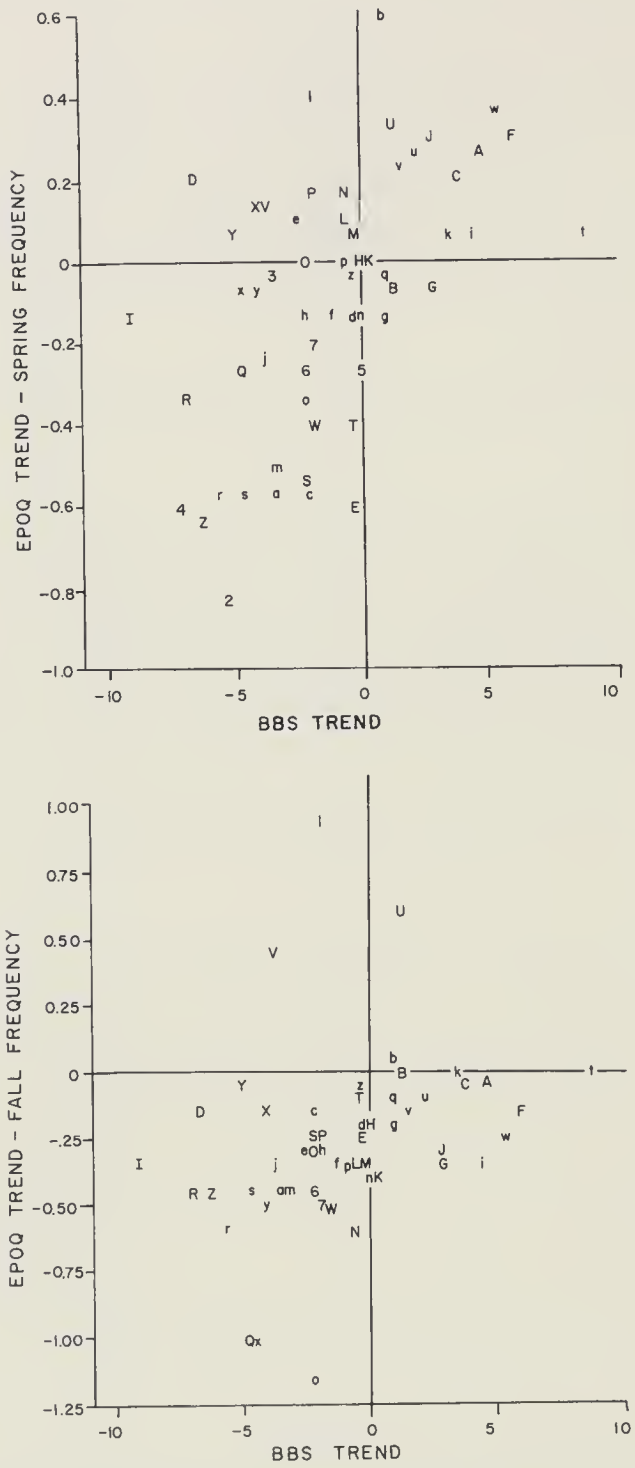

FIG. 2. Trends in date-adjusted frequency indices from ÉPOQ for spring (Part A, top) and fall (Part B, bottom) plotted against BBS trends. Trends expressed as annual percent change in abundance (BBS) and annual change in arcsin transformed annual percentages (see text). See Table 1 for species codes.

improve precision of trend estimates without altering long-term bias and, therefore, may not be worth the effort involved. Despite the bias, however, ÉPOQ abundance indices produced very few "false negatives" (Fig. 1). Thus, while an increasing trend in ÉPOQ does not necessarily indicate a true increase, a negative ÉPOQ trend based on abundance is evidently quite a reliable indicator that some kind of decline is actually taking place. (ÉPOQ frequency indices produced false negatives much more often; Fig. 2.) Declines are of more interest for conservation alerts than are increases, and checklist programs appear to offer a means of detecting some (though not all) declines in species that are poorly covered by standard population monitoring programs. It should therefore be of value to analyze ÉPOQ data from the migration season for species that breed primarily in tundra or northern boreal zones and for which we have no other data on population trend.

ACKNOWLEDGMENTS

Thanks are due to the thousands of dedicated birders and record-keepers in Quebec without whom this analysis could not have been attempted. Peter Blancher, Brenda Dale, and an anonymous reviewer made helpful comments on the manuscript.

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Wilson Bull., 108(3), 1996, pp. 550–555

EFFECT OF MATE REMOVAL ON SINGING BEHAVIOR AND MOVEMENT PATTERNS OF FEMALE NORTHERN CARDINALS

David B. McElroy and Gary Ritchison

Abstract.—We temporarily removed the mates of four female Northern Cardinals (*Cardinalis cardinalis*) during the pre-nesting period in an attempt to clarify the functions of singing by females. Mate removal had no significant effect on singing rates, number of movements per hour, or distance moved per hour. The failure to increase singing rates after mate removal suggests that singing by female cardinals is not used to attract new mates and the absence of any change in movement patterns suggests that females may not actively seek new mates. When singing, female cardinals were usually accompanied by a singing male and, prior to and after mate removal, females often duetted with their mates. Female cardinals may sing and duet with mates to advertise the presence of a female and the mated status of a male. Duetting may also permit pairs to learn each other's songs. Such learning may represent a form of investment important in maintaining a pair bond and may also, later in the season, permit more efficient intrapair communication. *Received 26 Oct. 1995, accepted 10 Feb. 1996.*

Although singing by females is now well documented in several species of passerines (e.g., Arcese et al. 1988, Johnson and Kermott 1990, Baptista et al. 1993), the functions of such singing often remain unclear. Most suggested functions have been based largely on observations, and few investigators have used experimentation. When used, experimentation has been limited to playback experiments (e.g., Ritchison 1983, 1986; Arcese et al. 1988; Baptista et al. 1993). In contrast, investigators examining the singing behavior of male passerines have used a variety of experimental techniques, including mate removal experiments. In these studies, the singing behavior of males is observed prior to and after removal of mates. Typically, males increase singing rates after removal of their mates, suggesting that singing plays a role either in maintaining contact with mates or in attracting new mates (Wasserman 1977, Krebs et al. 1981, Cuthill and Hindmarsh 1985, Otter and Ratcliffe 1993).

Female Northern Cardinals (*Cardinalis cardinalis*) sing primarily during the period after males establish territories and before nesting begins (Ritchison 1986). Singing females usually are accompanied by singing mates (Lemon 1968, Ritchison 1986). Although these observations suggest that singing by female Northern Cardinals may be important in intrapair communication, perhaps playing some role in the formation of the pair bond (Ritchison 1986), additional information is needed. The objec-

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tive of our study was to use mate removal experiments in an attempt to clarify the functions of singing by female Northern Cardinals.

METHODS

We conducted this study during the pre-nesting periods (January through early May) of 1990, 1992, and 1993 at the Central Kentucky Wildlife Management Area located 17 km southeast of Richmond, Madison County, Kentucky. Male and female cardinals were captured in mist nets and individually marked with colored leg bands and plastic tape attached to the tail (Ritchison 1984). Beginning in March, marked cardinals were observed to determine the identity of pairs and the location and boundaries of territories. Paired females (N = 4) were subsequently re-captured and fitted with radio-transmitters. Removal experiments with these females began on 2 April and 20 April 1990, 19 April 1992, and 29 April 1993, respectively.

Experiments were divided into three periods: pre-removal, removal, and post-removal. Each period lasted two days and focal females were observed for three hours each day. All observations were made during the period from sunrise to 11:00. Pre-removal periods began no sooner than two days after females had been fitted with transmitters. After the pre-removal period, the female's mate was captured by luring him into a mist net using the playback of cardinal songs. During the two-day removal period, males were kept in the lab in a wire mesh cage and provided food and water. The post-removal period began with the release of the male.

The movements of focal females were monitored using a receiver (Telonic's TR-2) with a two-element antenna. The focal female's location was marked on a map of the study area every 15 min. All songs were recorded using a Uher 4000 Report Monitor tape recorder with a Dan Gibson parabolic microphone or a Marantz recorder with a directional microphone. Observations and recordings of females were made from a distance of 20 m or more.

Recordings were analyzed using a Kay Elemetrics Sonagraph (Model 5500). For each observation period, we noted the number of songs and number of bouts, with a bout defined as a series of songs separated by intervals less than 30 sec. For each song, we determined the song type (see figures 1 and 2 in Ritchison 1988), number of syllables, and duration. Each bout was classified as either an accompanied bout or a non-accompanied bout, with an accompanied bout defined as a bout during which a conspecific male (either in the female's territory or in an adjacent territory) sang at some time during the bout. Bouts of female song during which their mates also sang were classified as duetting bouts.

Possible differences among periods for all variables were tested using repeated measures analysis of variance (SAS 1989). Repeated measures analysis provides a test for interactions (Beal and Khamis 1990), and we also examined possible interactions between individuals and periods. Tests for non-random use of song types were made using likelihood ratio chi-square tests (SAS 1989). All values are presented as means ± one standard error.

RESULTS

The singing rates of female cardinals did not vary significantly among test periods ($F = 1.34$, $P = 0.34$), with no significant interaction between individual and period ($F = 1.53$, $P = 0.21$). Females uttered an average of 20.6 ± 4.1 songs/h during the pre-removal period, 20.1 ± 6.5 songs/h during the removal period, and 22.7 ± 8.8 songs/h during the post-removal period.

Female cardinals exhibited no significant variation among periods in

the number of syllables per song ($F = 1.93$, $P = 0.24$). We found a significant interaction between individual and period ($F = 2.47$, $P = 0.03$), however, no clear trend was apparent. Two females used songs with more syllables during the removal period, one female uttered songs with more syllables during the post-removal period (although this female sang only 11 songs during the pre-removal and removal periods), and the songs of the fourth female showed little variation in number of syllables per song among periods.

Female cardinals exhibited no significant variation among periods in song duration ($F = 0.6$, $P = 0.58$), with no significant interaction between individual and period ($F = 1.67$, $P = 0.14$). Also, we found no significant differences among periods in intersong intervals ($F = 0.21$, $P = 0.82$). There was a significant interaction between individual and period ($F = 4.7$, $P = 0.0003$), however, no clear trends were apparent. Three females exhibited little variation in intersong intervals among periods while intersong intervals for the fourth female were longer during the removal and post-removal periods than during the pre-removal period.

All four female cardinals exhibited significant variation (likelihood ratio tests, $P < 0.0001$) in the use of song types during the three periods. However, no consistent trends were found among the four females in the use of particular song types during particular periods.

During most bouts of song (N = 172 of 248 or 69.4%), female cardinals were accompanied by singing males, either their mate (duetting bouts) or another conspecific male. Females sang with their mates during 88 bouts and with other conspecific males during 84 bouts. During seven bouts, females sang with both their mate and an intruding male. Females were accompanied by males in 69 bouts during the pre-removal period, 46 during the removal period, and 57 during the post-removal period. The number of non-accompanied bouts declined from 45 during the pre-removal period to 18 during the removal period to 13 during the post-removal period.

Female cardinals showed no significant variation among periods either in number of movements per hour ($F = 1.57$, $P = 0.3$) or distance moved per hour ($F = 0.14$, $P = 0.63$). No significant interactions were noted for either movements per hour ($F = 0.36$, $P = 0.87$) or distance moved per hour ($F = 0.69$, $P = 0.63$). For all females and periods combined, the mean number of movements per hour was 4.07 ± 2.65 while the mean distance moved per hour was 109.5 ± 59.4 m. All four females remained on their respective territories after removal of their mates.

Trespassing by conspecific males occurred significantly more often during the removal period ($F = 19.6$, $P = 0.004$), with an average of 3.16 ± 1.02 intrusions per hour during the removal period, 0.46 ± 0.26 intru-

sions per hour during the pre-removal period, and 2.49 ± 1.11 intrusions per hour during the post-removal period. The number of singing bouts by intruding males in the territories of focal females varied significantly among periods ($F = 28.8$, $P = 0.0018$), with an average of 1.64 ± 0.35 bouts/h during the removal period, 0.09 ± 0.05 bouts/h during pre-removal, and 1.07 ± 0.42 bouts/h during post-removal. Focal females sang with intruding males an average of 0.6 ± 0.19 times/h during removal and 0.19 ± 0.04 times/h during post-removal, a significant difference ($F = 12.6$, $P = 0.011$). No singing with intruders occurred during the pre-removal period.

Three temporarily-removed males maintained their territories and their mates after being released. One male lost his territory and his mate to another male during the removal period and was unable to reclaim either after release.

DISCUSSION

Female Northern Cardinals in our study did not increase singing rates when mates were removed. In contrast, passerine males typically increase singing rates after removal of a mate (Wasserman 1977, Krebs et al. 1981, Cuthill and Hindmarsh 1985, Otter and Ratcliffe 1993). Increased song output following mate removal may indicate an attempt to re-establish contact with the absent mate or to attract a new mate (Krebs et al. 1981). Johnson and Kermott (1990) found that female House Wrens (*Troglodytes aedon*) sang primarily after losing contact with mates and these songs appeared to redirect a mate's attention to the singing female. Such behavior was not observed in our study, and this failure to increase singing rates after removal of mates suggests that singing by female cardinals is not used to establish or maintain contact with mates.

There is little evidence that passerine females sing to attract new mates. Baptista et al. (1993) reported that one widowed female White-crowned Sparrow (*Zonotrichiz leucophrys*) produced long bouts of loud song and suggested that she may have been advertising for a mate. Female Northern Cardinals did not increase song output after mate removal, and this suggests that singing by female cardinals is not used to attract new mates.

Female cardinals in our study exhibited no significant changes among periods in either number of movements or distance moved per hour. In contrast, Klatt and Ritchison (1994) found that female Eastern Screech-Owls (*Otus asio*) made significantly more movements and moved significantly greater distances after mate removal and suggested that such behavior would increase the chances either of re-establishing contact with a mate or attracting a new mate. The absence of any change in movement patterns after mate removal suggests that female cardinals may not ac-

tively seek either to re-establish contact with a mate or attract a new mate. Rather, females may use a more passive approach. The absence of a territorial male, as during the removal periods in our study, may indicate to other males the availability of a territory and, perhaps, of a female. Female cardinals may wait for neighboring or floater males to trespass, then seek to pair with the male that eventually obtains the territory.

Our results indicate that singing by female cardinals does not deter male intrusion into a female's territory. Male intrusion rates increased during the removal period even though females continued to sing. Female song may, however, deter trespassing by other females. If singing by females is directed primarily to conspecific females, then rates would not be expected to increase in the absence of the male. Thus, female cardinals may sing, and duet with mates, to advertise the presence of a female and, perhaps, the mated status of a male. In further support of this hypothesis, songs uttered by cardinals during duets are typically normal or high volume songs that can be heard in neighboring territories (pers. observ.). Such advertisement may be important in mate retention because unpaired females (floaters) are present in our cardinal population (Ritchison et al. 1994). Further, some male cardinals participate in extra-pair copulations (EPCs) (Ritchison et al. 1994). Female cardinals may reduce the likelihood that their mate will participate in EPCs by duetting with and advertising the mated status of their mate. Reduced participation in EPCs by mates may be beneficial to females because males that do not engage in EPCs (or engage in fewer EPCs) may provide more parental care (Westneat et al. 1990).

Singing by female Northern Cardinals may also permit pairs to learn each other's songs. Paired cardinals may sing from or near nests during the incubation and nestling periods, and Halkin (1990) proposed that female cardinals on the nest may match her mate's song type to inform the male that he need not visit (bring food to) the nest. For such communication to occur, paired cardinals must know the song type repertoires of their mates. Duetting prior to nesting may permit paired cardinals to become familiar with, and perhaps learn, song types in the repertoire of their mate. Lending support to this hypothesis, we found that male and female cardinals sometimes matched song types during duets (pers. obs.).

Matching song types during duets could also serve other functions. Learning a mate's song types may represent a form of investment that may be important in establishing and maintaining a pair bond (Wickler 1980). Thus, if male and female cardinals must learn the songs of their mates, then duetting may play a role in establishing and maintaining pair bonds.

In summary, our results suggest that female Northern Cardinals do not

sing to re-establish contact with an absent mate or to attract a new mate. Rather, female cardinals sing (and duet with mates) to advertise the females' presence and the paired status of her mate. Duetting may also permit paired cardinals to learn other's songs. Such learning may represent a form of investment important in maintaining a pair bond (Wickler 1980) and may also, later in the season, permit more efficient communication in the vicinity of nests (Halkin 1990).

ACKNOWLEDGMENTS

We thank Ken Yasukawa and an anonymous reviewer for helpful comments on the manuscript. Financial support was provided by Eastern Kentucky University.

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Wilson Bull., 108(3), 1996, pp. 556–566

RADIO TELEMETRY DOCUMENTS 24-HOUR FEEDING ACTIVITY OF WINTERING LESSER SCAUP

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ABSTRACT.—We used radio telemetry to record 198 h of feeding behavior of five Lesser Scaup (*Aythya affinis*) on the Indiana Harbor Canal in northwestern Indiana during January and February 1994. Lesser Scaup fed for short periods of time intermittently during each 24-h period. Lesser Scaup fed a total of 96 min during the day and 226 min during the night. They fed more between sunset and midnight (31.9% of the period, $P = 0.003$) than between sunrise and noon (11.6%) or noon and sunset (19.5%); time spent feeding between midnight and sunrise (26.3%) did not differ from other times of day. Mean dive duration (22.9 ± 0.64 sec) did not vary by time of day ($P = 0.186$–0.744). These results are the first 24-h feeding activity reported for individually marked Lesser Scaup. *Received 27 Sept. 1995, accepted 3 Feb. 1996.*

Knowledge of both diurnal and nocturnal activity is needed to understand the use of time and energy by waterfowl (Jorde and Owen 1988). However, estimates of 24-h activity of waterfowl, especially diving ducks, generally are difficult to obtain and often are imprecise. Night-vision light intensifiers (NVLI) have been used to document nocturnal activity based on scan census or focal animal observations (Tamsier 1976, Jorde et al. 1983, Paulus 1984, Takekawa 1987, Bergan et al. 1989). Night observations, however, are often limited by access and viewing area (Jorde and Owen 1988, Bergan et al. 1989). Scan counts underestimate feeding activity for diving ducks, because some birds are underwater during the scan (Siegfried 1974). Also, studies of diving ducks using focal animal methods are impossible to conduct in many situations because it is difficult to keep track of individual birds in large flocks (C. Custer, pers. obs.).

Few studies have recorded 24-h activity budgets of Lesser Scaup (*Aythya affinis*). Wintering male Lesser Scaup in South Carolina spent <10% of their time feeding at night and approximately 40% of the day feeding (Bergan et al. 1989); data were collected using focal-animal sampling (5-min duration/bird) and NVLI. In contrast, wintering Lesser Scaup on the Mississippi River in Wisconsin spent 28% of the night feeding and 16% of the day; data were collected using modified scan sampling and NVLI (Takekawa 1987). We are aware of only one study that quantified 24-h activity budgets of individual waterfowl. The activities of a single breeding male European Pochard (*Aythya ferina*) were recorded through-

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out one 24-h period with the aid of a field glass of high luminosity on a bright moonlight night (Klíma 1966).

The attenuation of radio signal strength has been used with penguins to quantify timing and duration of feeding behavior (Trivelpiece et al. 1986). Radio telemetry has not been used to quantify feeding of diving ducks, however. Our objective was to quantify 24-h feeding activity of Lesser Scaup wintering on the Indiana Harbor Canal (IHC) (41°38′N 87°28′W) using radio telemetry.

STUDY AREA AND METHODS

The IHC and Grand Calumet River system (Fig. 1) contains some of the last remaining wildlife habitat within the urban, industrial corridor that dominates the south shore of Lake Michigan (Brock 1986). Only 50 of 10,000 acres of inland beach-ridge dune and swale habitat still remain (Bacone 1979), and these wetlands along with the Grand Calumet River and IHC provide resting, feeding, and loafing habitat for migrating and wintering birds (Brock 1986), and breeding habitat for Black-crowned Night-Herons (*Nycticorax nycticorax*), Barn Swallows (*Hirundo rustica*), Herring Gulls (*Larus argentatus*), and Mallards (*Anas platyrhynchos*). During winter, the IHC is routinely used by 200–300 Lesser Scaup (J. Simesko, Lake Dock Co., pers. comm.; Custer et al. 1996). Indiana Harbor Canal was constructed in the early 1900s for navigation and to carry waste discharges from 30 outlets to Lake Michigan (Bolts 1993). The physical structure of IHC, <50-m wide, open water, and unlimited access to some observation sites enabled us to monitor 24-h activity budgets. From the trap site out to Lake Michigan, IHC has straight-sided concrete/steel walls and is >3m deep with no rooted, submergent vegetation. South of the trap site, soil banks predominate. The banks slope gradually into the water which becomes shallower (<1.5 m deep) and supports some aquatic vegetation.

We implanted radio transmitters (164–167 Mhz) in the abdominal cavity (N = 10) or subcutaneously (N = 2) in 12 male Lesser Scaup trapped in a baited, swim-in corral trap (Haramis et al. 1987) in IHC (Fig. 1). We stopped trapping after our scaup were radio marked. Abdominal implants, procured from Advanced Telemetry Systems Inc., were cylindrical (50-mm long, 20-mm diameter) with an internal, coiled antenna and weighed about 20 g. Subcutaneous implants, Holohil Systems Ltd., were disc-shaped (20-mm diameter, 8-mm thick) and implanted in the upper back with an external flexible antenna and weighed about 5 g. The heaviest transmitter weighed ≤3% of the duck's body weight. We implanted all transmitters within 5 h starting at 20:00 CST, 6 January 1994, and released the scaup at the trap site at 10:00, 7 January. The transmitters were implanted under sterile conditions; scaup were anesthetized with isoflurane, the transmitter implanted, and the duck immediately revived with 100% oxygen (Olsen et al. 1992, Korschgen, pers. comm.). We followed approved Animal Care and Use protocols of Northern Prairie Science Center, Jamestown, North Dakota. We assumed that the Lesser Scaup we trapped were representative of the flock present in IHC during this study.

Before establishing data collection protocols, we observed general feeding patterns of Lesser Scaup for several hours. We found that Lesser Scaup fed while diving in one area or while slowly swimming, dived and surfaced in a consistent pattern of underwater and surface times, and did not interrupt feeding with preening, bathing, resting, or other behaviors. Feeding individuals were usually ≥10 m from roosting and resting flocks of Lesser Scaup and rejoined these flocks after feeding.

We used changes in radio signal strength to determine when a radio-marked Lesser Scaup

FIG. 1. The Grand Calumet River–Indiana Harbor Canal study area, East Chicago, Indiana, showing the trap site and behavioral observation sites, January–February, 1994.

was feeding, i.e., no signal or a weak signal was received when the duck was under water (Trivelpiece et al. 1986). Visual observations of a radio-marked Lesser Scaup confirmed that dives inferred by signal strength were actually dives.

To select an appropriate observation interval to monitor feeding behavior, we listened to signals from three feeding Lesser Scaup continually for ≥30 min each and another radio-marked scaup for 5 h. Bouts of feeding (N = 15) lasted 11.1 ± 1.39 min (± 1 SE); therefore, we selected 10 min intervals as the minimum needed to detect feeding behavior.

We established behavioral observation sites at four of 15 locations (Fig. 1) because we had 24-h access to these four sites. Additionally, these sites were where many of the radio-marked scaup spent the winter (Custer et al. 1996). On days that we recorded behavior, we checked each site until we located one or more radio-marked Lesser Scaup. There were usually ≤3 radio-marked Lesser Scaup at a site. We collected behavioral data on the radio-marked scaup using two methods: 10-min scans and focal-animal sampling (Altmann 1974). We collected 10-min scan data to estimate percent of time spent foraging. We listened to each radio signal for 2 min at 10-min intervals and determined whether the duck was feeding (diving) or not feeding. The rhythmic pattern of ducks diving to feed allowed us to differentiate feeding activity from random changes in signal strength or temporary loss of signal (Kenward 1987:130). Secondly, we used focal animal sampling to quantify the duration of foraging dives. Between 10-min scans, we selected a feeding duck and recorded for 3–6 min the time it spent above and below the water's surface while feeding. When more than one scaup was feeding, we alternated focal animal observations equally among the scaup present.

Behavior was recorded by human observers or by video taping the radio receiver. During video recordings, we programmed the radio receiver to scan 4–5 frequencies sequentially for 2 min each. A camcorder was focused on the radio receiver's display and thus recorded both the monitored frequency and the audio speaker sounds. The camcorder also recorded the time of day. Only observations of radio-marked birds whose behaviors were recorded continuously for ≥4 h (N = 5 scaup) were included in the analyses. The other seven radio-marked scaup were located only infrequently or in areas where we could not record continuous behavioral observations.

We recorded behavior during four periods: morning (sunrise to 12:00 h CST), afternoon (12:01 h to sunset), evening (sunset to 24:00 h), and night (00:01 h to sunrise). Duration of time periods ranged from 5 h–5 h 20 min for daylight periods and 6 h 20 min–6 h 40 min during evenings and nights.

For each scaup, we calculated the frequency of consecutive 10-min scans during which it was feeding and not feeding during each time period. We analyzed frequency data by time period and by duck with Fisher's Exact Tests (Zar 1984). Categories for number of consecutive 10-min scans during which an individual was feeding were 1, 2, and 3+. Three or more consecutive scans were combined into one category for frequency analyses to reduce the number of cells with zeros. When the overall Fisher's Exact Test was significant, all pairwise combinations were tested to determine which frequencies differed. An alpha of 0.005 was used for pairwise Fisher's Exact Test comparisons to give an overall $P < 0.05$ (Neter et al. 1985). We pooled 1 and 2, 3 and 4, 5 and 6, and 7+ consecutive 10-min scans without feeding for statistical tests to reduce the number of cells with zeros.

Percent of time spent feeding during each time period by each duck was calculated from the 10-min scan data (Altmann 1974). A fixed-effect, 2-way analysis of variance (ANOVA) model was used to compare the average percent of time spent feeding among ducks and time periods. We used Bartlett's test to test the homogeneity of variance assumption of ANOVA (Zar 1984:181). When variances were not homogeneous, percents were square-root arcsine transformed. Untransformed percents ±1 SE are presented in text and tables.

Repeated measures statistics were not possible with these data; therefore, all data were analyzed and presented by individual duck to account for individual variation. We used an alpha of 0.05 for all ANOVAs.

We used one-way ANOVA to test our null hypothesis that average time (sec) spent underwater per dive searching for and retrieving food did not differ among time periods or among ducks. Empty cells precluded using 2-way ANOVA. Because there were no time differences, we combined all time periods and tested for differences among individuals.

RESULTS

We recorded 198 h of behavior on five radio-marked Lesser Scaup between 27 January and 16 February 1994 in IHC. Weather patterns during the study were normal; daily maximum temperatures were between −10° and 0°C with occasional snowfall. The normal high temperature for February is −2°C (Bair 1992).

Lesser Scaup fed intermittently for short periods throughout the 24-h period (Fig. 2). As an example, Lesser Scaup #4566 fed during nine 10-min scan periods between sunset and midnight on 2 February; the first feeding bout lasted for two consecutive 10-min scans (Fig. 2). The modal number of consecutive 10-min scans during which Lesser Scaup were feeding was one for four of five Lesser Scaup (Table 1). Lesser Scaup #4666 differed from the other four scaup (pairwise Fisher's Exact Test, all Ps ≤ 0.002) with a mode of 3+ consecutive 10-min scans with feeding (Table 1). The median number of consecutive feeding bouts for all scaup combined was one. Frequency of consecutive 10-min scans with feeding did not vary by time period (3 × 4 Fisher's Exact Test, $P = 0.716$, N = 98); feeding bouts were not longer or shorter during any particular time period.

The number of consecutive 10-min scans without feeding did not differ among ducks (Table 1) or among time periods (4 × 4 Fisher's Exact Test $P = 0.318$, N = 98). The median number of consecutive scans without feeding was four for all scaup and time periods combined.

Lesser Scaup fed for 23.7 ± 2.5% (SE) of each 24-h day. They spent a greater proportion of their time feeding during the evening period (31.9 ± 5.07%, N = 16 evening periods) than during the morning (11.6 ± 2.60%, N = 9) or afternoon periods (19.5 ± 4.62%, N = 13). Proportion of time spent feeding during the night (26.3 ± 4.16%, N = 13) did not differ from the other three time periods ($F = 5.75$; df = 3,33; $P = 0.003$). The time spent feeding varied among individuals (Table 2), but there was no interaction between time period and individual duck ($F = 0.89$; df = 10,33; $P = 0.548$).

Time spent underwater per dive to search for and retrieve food did not differ among the four time periods (22.9 ± 0.64 sec, N = 57; Ps 0.186

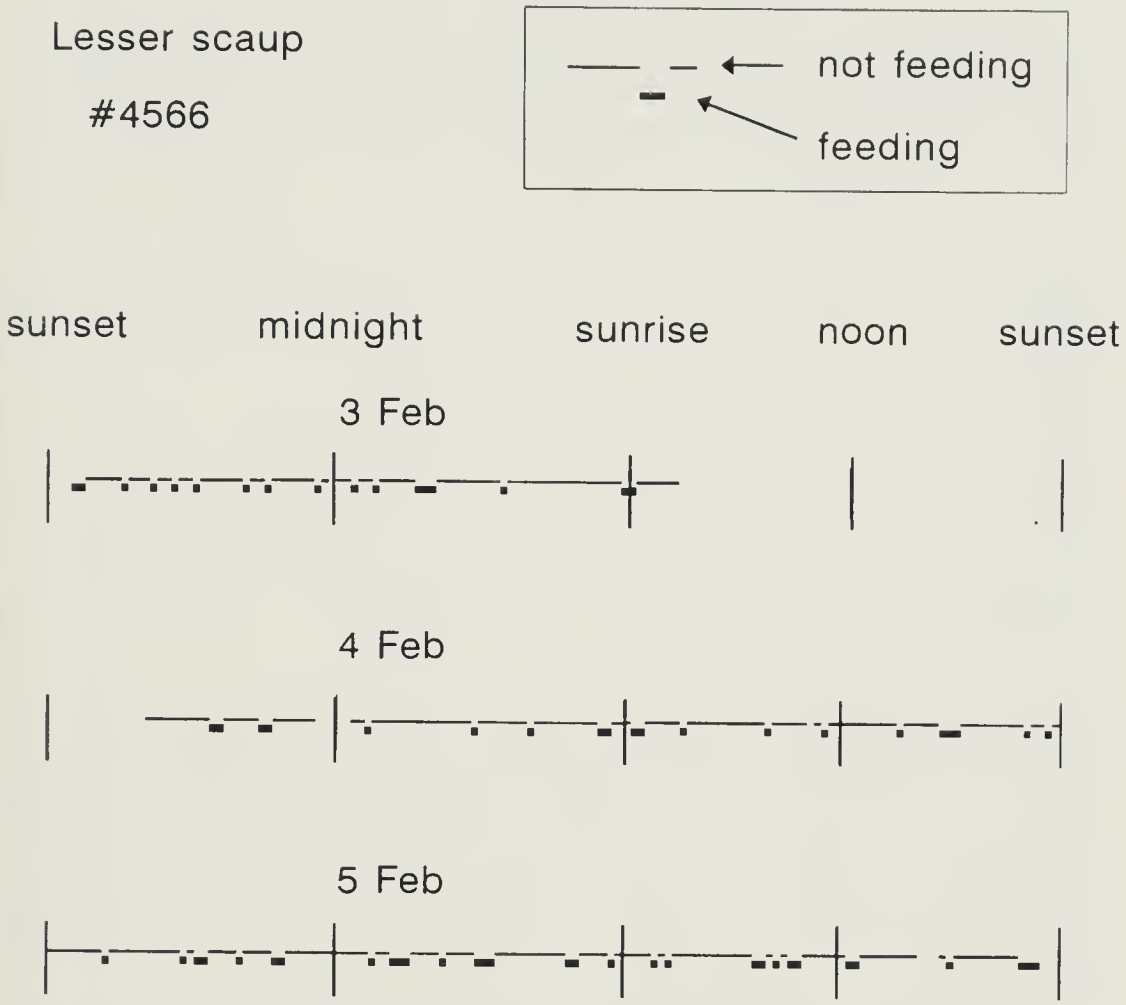

FIG. 2. Summary of 40+ consecutive hours of 10-min behavior scans for Lesser Scaup #4566 in Indiana Harbor Canal, East Chicago, Indiana, 2–5 February 1994.

− 0.744). Bird #4566 spent significantly less time underwater than bird #4616 or bird #4666 (Table 2), however.

DISCUSSION

Our study further demonstrates the need to collect nocturnal data to better understand the feeding ecology of Lesser Scaup. On some wintering areas, feeding is more prevalent at night than during the day (Takekawa 1987 and this study). The proportion of time spent feeding during nocturnal hours (29%) and diurnal hours (16%) in IHC was strikingly similar to that of Lesser Scaup on the Mississippi River in Wisconsin which spent 28% of the night feeding and 16% of the day (Takekawa 1987). Tufted ducks (*Aythya fuligula*) in Switzerland, a closely related species, also spent a higher proportion of the night feeding (30–50% of the night) than they did during the day (<10% of the day) (Pedroli 1982). In contrast,

TABLE 1

NUMBER OF CONSECUTIVE 10-MIN SCANS DURING WHICH RADIO-MARKED LESSER SCAUP WERE FEEDING AND NOT FEEDING IN INDIANA HARBOR CANAL, EAST CHICAGO, INDIANA, JANUARY–FEBRUARY 1994

Transmitter frequency	Consecutive 10-min scans								
	Feeding				Not feeding				
	1	2	3+		1–2	3–4	5–6	7+	
4566	32	17	4	A[a]	10	8	10	19	A[b]
4616	7	2	2	AB	5	2	1	4	A
7029	8	1	0	AB	2	1	1	2	A
4637	7	0	5	B	4	3	0	3	A
4666	0	5	8	C	4	4	1	2	A

[a] Frequency distributions sharing same letter are not different among Lesser Scaup, 3 × 5 Fisher's Exact Test ($P < 0.001$). Pairwise comparisons to separate individual Lesser Scaup were considered significant at $P < 0.005$ for an experiment-wide alpha level of $P \leq 0.05$.

[b] 4 × 5 Fisher's Exact Test ($P = 0.699$).

male Lesser Scaup in South Carolina fed <10% of the night and approximately 40% of the day (Bergan et al. 1989). Human disturbance is often cited as the reason for nocturnal feeding (McNeil et al. 1992). Our study and the study in South Carolina, however, were conducted in areas with little human disturbance; therefore, this would not explain the difference between the two studies. Neither cold temperatures (down to −10°C) nor precipitation affected percent of time spent feeding (Cronan 1957, Noseworthy 1981, Takekawa 1987), so temperature should not be a factor when comparing these two studies.

Although the percent of time spent feeding during day and night in the

TABLE 2

AVERAGE TIME SPENT FEEDING AND TIME SPENT UNDERWATER PER DIVE BY RADIO-MARKED LESSER SCAUP IN INDIANA HARBOR CANAL, EAST CHICAGO, INDIANA DURING JANUARY AND FEBRUARY 1994

Transmitter number	Time feeding (%)				Time underwater (sec)			
	Mean		SE	N[a]	Mean		SE	N[a]
4666	39.2	A[b]	6.67	11	25.0	A[c]	0.82	24
4637	36.7	AC	7.04	6	22.9	AB	1.41	8
4566	17.5	BC	1.86	20	19.4	B	0.92	20
4616	17.4	B	4.69	10	26.3	A	2.43	5
7029	9.0	BC	2.12	4				

[a] N = number of time-of-day periods for which percent of time spent feeding or time underwater was calculated.

[b] Means sharing same letter are not different ($F = 5.60$; df = 4,33; $P = 0.002$).

[c] Means sharing same letter are not different ($F = 7.90$; df = 3,53; $P < 0.001$).

IHC was different from some other studies, the total amount of time spent feeding (5.7 h/d) in IHC was similar to Lesser Scaup in South Carolina (4 h/d) (Bergan et al. 1989), Lesser Scaup on the Mississippi River (4.1 h/d) (Takekawa 1987), and Tufted Ducks in Switzerland (4.8–5.2 h/d) (Pedroli 1982).

Lesser Scaup feed for short periods of time (median number of consecutive scans with feeding was one) followed by longer non-feeding periods (median number of consecutive non-feeding scans was 4). The average length of a feeding bout was 11.1 min. We had the longest continuous record on scaup #4566, which demonstrated this intermittent feeding pattern continually for two days. The feeding patterns of the other four Lesser Scaup, although less extensive, were consistent with the pattern of #4566.

During the pre-breeding season (May) in Manitoba, Lesser Scaup repeated a foraging, bathing/preening, resting/sleeping cycle about every 3 h during daylight hours (Siegfried 1974), which was longer than the approximately 1-h cycle we found in IHC during winter. European Pochards in the Bohemian highlands also had a 3–4 h activity which was repeated regularly during a 24-h period during spring (Klíma 1966). Klíma (1966) hypothesized that the open water habitat with its lack of microhabitat variation, minimal human disturbance, lack of phototaxis in prey behavior, and tactile feeding by European Pochards contributed to the similarity of diurnal and nocturnal feeding patterns. Several characteristics of IHC are similar to that of Bohemia; IHC is a relatively undisturbed location without hunting and has little recreational or public use. The scaup seem to have habituated to the industrialized setting, and the bright lights mimic moon-lit nights which are conducive to nocturnal feeding (Adair 1990: 73). Most of the IHC is deep (>3 m) open water, and availability of benthic prey, mainly oligochaete worms (T. W. Custer, Natl. Biol. Serv., unpubl. data), does not vary by time of day (R. Whitman, pers. comm.). Duration of feeding cycles may be a function of the type of prey consumed and the time needed to handle, process, and digest it. Oligochaetes are easy to capture, are very soft, and should be processed through the digestive system more quickly than other more traditional Lesser Scaup food items such as molluscs and arthropods (Swanson and Bartonek 1970, Afton et al. 1991, Custer and Custer 1996).

Time spent underwater per dive ($\bar{x}$ = 23 sec) by Lesser Scaup in our study was similar to that of Lesser Scaup wintering in Chesapeake Bay ($\bar{x}$ = 23.6 sec, G. M. Haramis, Natl. Biol. Ser., pers. comm.) and by Lesser and Greater scaup wintering in Connecticut ($\bar{x}$ = 20.4 sec) (Cronan 1957). However, shorter dive times have been reported for Lesser Scaup in Manitoba during spring ($\bar{x}$ = 10 sec) (Siegfried 1974, 1976); Lesser and Great-

er Scaup in the Detroit River ($\bar{x}$ = 16.4 sec) (Noseworthy 1981); and Lesser Scaup in South Carolina ($\bar{x}$ = 16.6 sec) (Alexander and Hair 1977). Time spent underwater is not related to water depth (Siegfried 1974) but may be a function of type and abundance of prey being exploited (Noseworthy 1981). Dive time may also be a function of individual behavior that affects distance covered per foot stroke, i.e. diving efficiency (Lovvorn et al. 1991). We do not believe that Lesser Scaup used visual cues to find food in IHC because they feed extensively at night and because of the similarity in time spent underwater searching and capturing prey during the day and night.

We feel that the behavior of these five individuals was representative of the approximately 200 Lesser Scaup (Custer et al. 1996) that wintered in IHC. Food was plentiful (>400,000 oligochaetes/m^2) in the area where we made out behavior observations (U.S. Fish and Wildlife Service-Battelle 1993), and we did not observe overt aggressive behavior (CMC, pers. obs.) that might indicate an abnormal situation. Scaup did not defend foraging sites during winter in South Carolina (Alexander and Hair 1977) and aggressive interactions were uncommon (Alexander and Hair 1977, Bergan et al. 1989).

Radio telemetry is an effective technique to monitor feeding behavior in diving ducks. We were able to recognize individual ducks and use a video recorder to acquire data remotely, an important consideration when continuous 24-h data are needed and availability of personnel is limited. Radio telemetry overcomes (1) the limitations of night-vision light intensifiers (Bergan et al. 1989) and collecting data during inclement weather and other conditions of poor visibility, (2) the problem of locating birds during scan counts (Siegfried 1974), and (3) of keeping track of individuals in large flocks during focal animal observations.

ACKNOWLEDGMENTS

We thank Atlas Steel, Inland Steel, Lake Dock Company, LTV Steel, and Shell Oil Company for access to their properties; C. M. Chaffee, J. T. Conomy, R. K. Hines, C. O. Kochanny, and A. D. Spicer for help with field work, K. P. Kenow for staying up most of one night implanting radio transmitters, C. E. Korschgen for advice on radio telemetry; and J. E. Austin, D. G. Jorde, K. P. Kenow, S. J. Maxson, T. C. Michot, K. J. Reinecke, E. J. Rockwell, and an anonymous reviewer for comments on earlier drafts of the manuscript.

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Wilson Bull., 108(3), 1996, pp. 567–572

BODY MASS AND CARCASS COMPOSITION OF FALL MIGRANT OLDSQUAWS

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ABSTRACT.—We investigated body and organ mass and carcass composition of twenty-seven migrant Oldsquaws (*Clangula hyemalis*) killed when they collided with power transmission lines in northeastern Ontario in October 1986. Comparison of the first principal component (PC1) from eight structural measurements indicated that adult male Oldsquaws were structurally larger than females; however, organ weights did not differ between sexes when PC1 was included as a covariate (ANCOVA, $P > 0.05$ in all cases). Carcass composition was similar to that reported for spring migrants. Ash-free lean dry weight (AFLDW) and ash were positively related to structural size, but did not differ between sexes when PC1 was included as a covariate. Lipids comprised 17.5% of whole body mass of females and 14.1% of males and were sufficient to fuel migration at least to the next likely staging area in the Great Lakes. Fall migrant Oldsquaws must have stored substantial lipid and protein reserves after breeding, suggesting that offshore feeding areas in James and Hudson Bay are critical. *Received 9 Oct. 1995, accepted 1 Feb. 1996.*

Oldsquaws (*Clangula hyemalis*) are small-bodied sea ducks that breed around Hudson Bay and across the Arctic and winter along the Atlantic and Pacific coasts and on the Great Lakes (Bellrose 1978). Peterson and Ellarson (1979) reported changes in carcass mass and composition of Oldsquaws between December and July. Their data were collected from wintering birds drowned in gill nets on Lake Michigan and from birds shot on a breeding area in northwest Hudson Bay. They found two peaks in carcass mass that were primarily associated with increased lipid deposits. Peak body mass occurred just before spring migration in May and in January, a time when Oldsquaws sometimes endure periods of thermal stress caused by low temperatures (Peterson and Ellarson 1979). However, carcass composition and body mass data are not available for Oldsquaws during the postbreeding period and fall migration. It is important to understand changes in body mass and carcass composition throughout the annual cycle to identify critical periods for weight gain. The purposes of this paper are to report body size and carcass composition for a sample of Oldsquaws obtained during fall migration in northeastern Ontario and to compare our data to those from Peterson and Ellarson (1979).

METHODS

We obtained 27 adult Oldsquaw carcasses from the Smoky Falls hydroelectric dam located on the west bank of the Mattagami River in northeastern Ontario (50°04′N, 82°10′W). The

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birds were killed during an apparent migration movement at around 22:00 h on 26 October 1986 when they hit power transmission lines spanning the river. All birds were frozen and shipped to the University of Western Ontario for carcass analysis. Whole Oldsquaw carcasses were thawed and weighed to the nearest 0.1 g (hereafter referred to as whole body mass) on a Mettler digital balance. Following Dzubin and Cooch (1992), we measured bill depth at the base, maximum bill width, culmen 1, tarsus bone, and exposed keel lengths to the nearest 0.1 mm, using Vernier calipers, and wing chord and total body length to the nearest mm using a ruler. We also measured wing length, from the body to the distal end of the outstretched wing, to the nearest mm using a ruler. Next we obtained carcass mass (whole body minus head, feet, wings, feathers, gastrointestinal tract, and reproductive organs) for comparison to data presented by Peterson and Ellarson (1979). All internal organs (except lungs and kidneys) and abdominal fat were dissected from the carcasses, patted dry with paper towels, and weighed to the nearest 0.01 g; contents were removed from gastrointestinal organs before weighing.

Our carcass composition analyses were designed to provide data comparable to those of Peterson and Ellarson (1979), but we also analyzed breast, leg, and liver tissues separately and included results from a combined homogenate of the head, feet, wings, feathers, gastrointestinal tract minus contents, and reproductive organs (hereafter called "dry parts"). The latter procedures provided data for whole birds for future comparisons. Combined values from breast, leg, liver, and carcass homogenate (but not dry parts) are equivalent to the "carcass" values from Peterson and Ellarson (1979). Samples were ground twice in a Hobart meat grinder and oven dried at 90°C to constant weight (Kerr et al. 1982). Dried carcass homogenate, dry parts homogenate, breast, leg, and liver samples were then homogenized separately in an electric coffee grinder. Lipid extractions were performed on subsamples (ca 10 g) of each constituent in a modified Soxhlet apparatus using petroleum ether as a solvent (Dobush et al. 1985). We determined the proportion of lipid in each subsample and multiplied this by the dry mass of each constituent sample to determine lipid mass. Lipid mass was then subtracted from dry weight of each constituent to estimate lean dry mass (LDM; Ankney and Afton 1988). Lean dry samples were ashed in a muffle furnace for 6 h at 550°C, and the proportion of ash in each was used to calculate ash for each constituent. Ash weight was subtracted from LDM to determine ash-free lean dry mass (AFLDM), a measure of total body protein.

To account for variation in carcass and component masses (lipid, AFLDM, ash) related to structural size, we used the correlation matrix from bill height, bill width, culmen, tarsus, wing chord, wing, body, and keel lengths in a principal components analysis (PCA) of all adults combined. From this we obtained scores for each bird along the first component axis (PC1) to use as an index of structural size (Alisauskas and Ankney 1987). PC1 accounted for 55% of variation in the characters measured, with a corresponding eigenvalue of 4.44. Loadings on the first principal component were all positive and ranged from 0.15 for culmen to 0.44 for wing chord. PC1 scores for individual ducks were used as covariates in analyses of covariance (ANCOVA) comparing lipid, ash, and protein dry weights between sexes. This technique accounts for variation between sexes that occurs as a result of differences in body size (Alisauskas and Ankney 1987) and allows comparison of relative amounts of lipid, ash, and protein. We also compared our data to those from Peterson and Ellarson (1979).

RESULTS

Male Oldsquaws were larger than females in most external morphological measurements (Table 1). Masses of esophagus, heart, liver, and

TABLE 1

MEANS OF MORPHOLOGICAL VARIABLES FOR ADULT OLDSQUAWS COLLECTED IN OCTOBER 1986 IN NORTHEASTERN ONTARIO[ab]

Variable	Males (N = 15)[c]	Females (N = 12)
Whole body mass	862.8 (17.9)A	733.6 (11.6)B
Carcass mass	633.0 (16.8)A	573.5 (12.7)B
Body length	342.1 (2.5)A	320.1 (3.5)B
Wing length	327.9 (1.6)A	313.8 (1.3)B
Wing chord	223.2 (1.1)A	210.2 (1.1)B
Tarsus	35.6 (0.3)A	34.7 (0.3)B
Culmen	27.1 (0.3)A	26.5 (0.4)A
Bill height	16.4 (0.3)A	15.9 (0.3)A
Bill width	19.7 (0.2)A	18.2 (0.2)B
Keel length	109.2 (1.0)A	100.6 (0.6)B
PC1	1.68 (0.3)A	−1.99 (0.2)B

[a] Linear measurements in mm, mass in g, standard error in parentheses.
[b] Means followed by the same letter are not different between sexes, *t*-test, $P > 0.05$.
[c] $N = 13$ males for variables that include the head; two males were decapitated when found.

gizzard differed between sexes (Table 2) but not when PC1 was included as a covariate (ANCOVA, $P > 0.05$ in all cases). AFLDM and ASH were positively related to structural size and did not differ between sexes when PC1 was included as a covariate (ANCOVA, $P > 0.30$), although both were absolutely larger in males. There was no relationship between total

TABLE 2

MEAN LENGTHS AND FRESH MASS OF INTERNAL ORGANS OF ADULT OLDSQUAWS COLLECTED IN NORTHEASTERN ONTARIO IN OCTOBER 1986[ab]

Organ	Males (N = 15)	Females (N = 12)
Small intestine length	133.9 (4.1)A	128.6 (4.2)A
Mass	17.0 (0.9)A	15.5 (0.6)A
Large intestine length	6.6 (0.2)A	6.7 (0.2)A
Mass	1.5 (0.1)A	1.3 (0.1)A
Caecum length	12.4 (0.6)A	11.1 (0.6)A
Mass	0.7 (0.1)A	0.8 (0.1)A
Esophagus mass	8.1 (0.3)A	6.8 (0.2)B
Gizzard mass	17.0 (2.2)A	10.1 (1.2)B
Heart mass	10.5 (0.2)A	6.9 (0.2)B
Pancreas mass	2.4 (0.2)A	1.8 (0.2)A
Spleen mass	0.34 (0.07)A	0.34 (0.07)A
Liver mass	32.3 (1.6)A	25.7 (1.2)B

[a] Masses measured in g, lengths in cm, standard error in parentheses.
[b] Means followed by the same letter are not different between sexes, *t*-test ($P > 0.05$).

TABLE 3

MEAN MASS OF CARCASS COMPONENTS OF ADULT OLDSQUAWS COLLECTED IN NORTHEASTERN ONTARIO IN OCTOBER 1986[a]

	Lipid	AFLDM	Ash
		Males[b]	
Breast	2.26 (0.15)	19.97 (0.35)	—
Leg	1.56 (0.13)	5.06 (0.11)	—
Liver	0.89 (0.11)	9.46 (0.55)	—
Homogenate	117.20 (7.64)	105.84 (3.70)	19.87 (0.93)
Dry parts	15.56 (0.57)	29.42 (1.17)	7.71 (0.17)
Total	141.46 (8.39)	172.40 (4.51)	28.27 (0.95)
		Females	
Breast	1.94 (0.10)	17.34 (0.29)	—
Leg	1.33 (0.09)	4.46 (0.10)	—
Liver	0.64 (0.09)	7.67 (0.36)	—
Homogenate	124.60 (6.78)	80.08 (2.82)	15.99 (0.45)
Dry parts	13.19 (0.68)	23.99 (0.51)	6.48 (0.17)
Total	141.70 (7.00)	133.56 (2.92)	22.48 (0.47)

[a] Mass in grams (g), standard error in parentheses.
[b] $N = 13$ males for "dry parts" and "total" values because 2 males were decapitated when found.

lipid mass and body size (ANCOVA, $P > 0.75$). Furthermore, total lipid mass was almost identical between male and female Oldsquaws (Table 3) despite the smaller structural size of females. Lipids comprised 17.5% of whole body weights of females and 14.1% of males.

DISCUSSION

Oldsquaws nest in tundra habitats of southwestern Hudson Bay, and a migration corridor between James Bay and the Great Lakes has been postulated (Bellrose 1978). We found little published information on external morphological measurements and gut morphology of Oldsquaws, but we assume that our sample was unbiased and therefore representative of Oldsquaws that migrate through northeastern Ontario. Gut measurements were shorter than those reported by Goudie and Ryan (1991: Table 2) for a combined sample of male and female Oldsquaws collected in coastal Newfoundland during winter. Oldsquaws in Newfoundland fed mostly upon amphipods and isopods, but the diet of Oldsquaws staging in James Bay is unknown.

Mean carcass mass of fall migrant female Oldsquaws was similar to that of spring migrants, and about 70–200 g greater than that during midsummer and winter (Peterson and Ellarson 1979). Most seasonal variation in carcass mass of adult females was attributable to fluctuations in lipid

levels; protein reserves (as indexed by LDM) were about 25 g heavier during fall migration than in mid-summer but about 15 g less than in spring. Carcass mass of males was similar in spring and fall; lipid levels also were similar in spring and fall. Inexplicably, male Oldsquaws had about 25 g more protein reserves in fall than in spring (Peterson and Ellarson 1979).

Peterson and Ellarson (1979: Table 1) reported that adult female Oldsquaws lost about 95% of lipid reserves and 30% of LDW between spring migration and the start of brood rearing in late July. Our data indicated that fall migrant female Oldsquaws had lipid levels similar to those of spring migrants, but protein reserves were 11% smaller. This suggests that (1) substantial increases in lipid and protein stores occur between late July and October and that (2) female Oldsquaws increase protein reserves in spring, perhaps for egg production.

Carcass lipids of adult female Oldsquaws on Lake Michigan in December were about 44 g less than, and protein reserves were about equal to those of fall migrants, suggesting that lipids provided energy during migration. Peterson and Ellarson (1979:294) estimated that a migrating Oldsquaw metabolized about 25.76 kcal/h. Assuming stored fat yields 9.45 kcal/g and conversion efficiency is 100%, 44 g of fat yields enough energy to fly for about 16 h. If Oldsquaws fly at an average speed of about 80 km/h (Bellrose 1978: 385), an average female in our sample could travel about 1280 km on 44 g of fat. Carcass lipids of adult males followed the same pattern as females, averaging 47 g less in winter than in fall. In addition, they had about 25 g more lean dry mass in fall than birds sampled in December. The nearest wintering areas for Oldsquaws from lower James Bay are the lower Great Lakes, i.e., southern Lake Michigan, Lake Erie, and Lake Ontario (Bellrose 1978). As none of these locations is >1280 km from lower James Bay, Oldsquaws had more than sufficient reserves to reach those destinations. Our data suggest that offshore habitats in James Bay and Hudson Bay are important to postbreeding Oldsquaws for replenishment and storage of protein and lipid reserves before fall migration.

ACKNOWLEDGMENTS

This work was supported by the Ontario Ministry of Natural Resources and the Univ. of Western Ontario. Oldsquaws were collected under permit from the Canadian Wildlife Service.

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AVIAN NEST-SITE SELECTION AND NESTING SUCCESS IN TWO FLORIDA CITRUS GROVES

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ABSTRACT.—We studied nesting success and nest-site selection of Common Ground-Doves (*Columbina passerina*), Northern Mockingbirds (*Mimus polyglottos*), Brown Thrashers (*Toxostoma rufum*), and Northern Cardinals (*Cardinalis cardinalis*) in two Florida citrus groves in spring 1989. Predation resulted in the loss of more than half of all nests. Fish Crows (*Corvus ossifragus*) and rat snakes (*Elaphe obsoleta*) seemed to be the major predators. Nesting success differed between groves and may have resulted from differences in human activities, predator populations, or vegetation structure. Nesting success of Northern Cardinals and Brown Thrashers was lower than that reported in other studies and may have been below the replacement level. Northern Mockingbirds had the most open nest sites with the largest inter-canopy distances (spacing between tree canopies), whereas Brown Thrashers seemed to select areas of the groves with the greatest canopy closure. Northern Cardinals tended to select nest trees with full canopies, perhaps to increase nest concealment. Common Ground-Dove nests were supported by limbs with small angles (degrees deviation from horizontal) and the largest diameters. *Received 21 June, accepted 25 Jan. 1996.*

Citrus groves represent a substantial proportion of breeding habitat available to birds in Florida, yet nest-site selection and nesting success have not been studied in these groves. As Florida habitat is converted to agricultural and other domestic uses, birds are forced to nest in altered habitats for which they may be poorly adapted (e.g., Dow 1969a, Best and Rodenhouse 1984). Our objectives were to document nesting success and characterize nest-site selection in Florida citrus groves. We attempted to answer the following questions: What preferences do breeding birds show in selecting their nest sites? Is nesting success affected by nest-site selection and, if so, how? Are citrus groves suitable nesting habitat for songbirds?

STUDY AREAS AND METHODS

We used two citrus groves on Merritt Island in Brevard County, Florida for study sites. Study grove 1, about 71 ha, was privately owned and managed and was almost entirely planted with orange trees. Study grove 2 was part of the Merritt Island National Wildlife Refuge, was 45 ha, and had a mixture of orange and grapefruit trees. The major herbaceous vegetation in the citrus groves was guinea grass (*Panicum maximum*), poorman's pepper (*Lepidium virginicum*), day-flower (*Commelina diffusa*), Richardia (*Richardia* spp.), prickly sida (*Sida spinosa*), Bermudagrass (*Cynodon dactylon*), vaseygrass (*Paspallum urvellei*), and amaranth (*Amaranthus* spp.). We studied nests from mid-March through early June in 1989. Nests were found by systematically examining each tree in the groves four times

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during the study and by observing bird behavior such as nest building and food carrying. The location of each nest tree was marked on a map of the grove, and a tree adjacent to the nest tree was flagged with colored tape. Nests were monitored on alternate days until they were no longer active. The number and condition of the eggs or young were recorded during each nest visit. Inaccessible nests were checked by using a pole-mounted mirror, by climbing the nest tree, or by using a stepladder in the bed of a pickup truck. As part of a concurrent study, nestlings were weighed and measured during each visit until there was a risk of inducing premature fledging. Broods of Northern Cardinals (*Cardinalis cardinalis*) and Brown Thrashers (*Toxostoma rufum*) also were ligatured during the nestling period to collect food samples (see Johnson et al. 1980). To avoid attracting predators to the nest site, the young were processed at least 10 m from the nest.

Apparent nest success was determined for species with a combined total for both groves of five or more nests with known outcomes. A nest was considered successful if at least one nestling fledged. Nests believed to be deserted due to our monitoring activities were excluded from analyses. Nesting success also was determined by using the number of days of nest exposure (Mayfield 1975). Because the nesting cycles of species breeding in the groves differed in length and, hence, the number of exposure days, nesting success was calculated separately for each species with an adequate sample size. The computer program MICROMORT (Heisey and Fuller 1985) was used to calculate survival rates for the egg and nestling stages and for the entire nesting cycle.

We used chi Square contingency analysis (2×3) to test for differences in nesting outcomes between groves. Nests were classified as successful, failed due to predation, or failed due to other causes. Tests were made for all species combined (Common Ground-Doves [*Columbina passerina*], Brown Thrashers, Northern Mockingbirds [*Mimus polyglottos*], and Northern Cardinals) and for each species separately, except for the Northern Mockingbird where the sample size was too small for individual analysis. Red-winged Blackbirds (*Agelaius phoeniceus*) were excluded from both analyses because their nests were found only in Grove 2 in localized areas associated with drainage canals.

After a nest became inactive, we recorded variables characterizing the nest vicinity, nest substrate, and nest position within the substrate. Inter-canopy (between canopy perimeters) and inter-tree (between trunks) distances within and between tree rows were determined. The number of young trees or open spaces where a tree was missing in an area around the nest tree, which included the eight nearest trees, was used as a measure of the openness of the nest tree vicinity. In addition, herbaceous ground cover was sampled within a 1-m^2 quadrat placed 5 m from the trunk of the nest tree in each of the four cardinal directions. Within each quadrat, maximum herbaceous cover height was measured with a tape, and the percent coverages of herbaceous vegetation, bare ground, and plant litter were visually estimated. Citrus type (orange, grapefruit, or hybrid root stock), nest tree height, canopy diameter, and the openness of the nest tree canopy (a visual estimate of the percent closure of the entire canopy) were used to characterize the nest tree. The position of the nest within the substrate was characterized by nest height, relative nest height (the height of the nest divided by the height of the nest tree), the number of limbs supporting the nest, the angles (degrees deviation from horizontal) and diameters of the six largest supporting limbs, and the percent foliage density of the nest tree, estimated visually above and below the nest in the area immediately around the nest. Nest-site measurements also were recorded for nests abandoned before discovery if the species could be identified.

Means and variances were calculated for the variables characterizing the groves and the nest sites of Common Ground-Doves, Brown Thrashers, Northern Mockingbirds, and Northern Cardinals. A series of Student's *t*-tests was used to test for differences in variables between the two groves, between the nest sites and the groves in general, and among the

nest sites of the four species. Because sections within the groves were managed differently, tree age and height, canopy diameter, inter-canopy and inter-tree distances, and the amount of herbaceous growth varied. Groves were thus blocked by management units, and vegetation was randomly sampled within each unit. For the analyses, 25 samples were randomly selected from each plot; the distribution of the samples among the management units was proportional to their area. Student's *t*-tests also were used to test for differences in nest-site characteristics between successful and failed nests of Common Ground-Doves, Northern Cardinals, and the combined nests of Common Ground-Doves, Brown Thrashers, Northern Mockingbirds, and Northern Cardinals in Grove 1. (Sample sizes for Brown Thrashers and Northern Mockingbirds were too small for separate *t*-tests.) Similarly, successful and failed nests of Common Ground-Doves, Brown Thrashers, Northern Cardinals, and the combined nests of Common Ground-Doves, Brown Thrashers, Northern Mockingbirds, and Northern Cardinals were compared in Grove 2. All significant relationships are presented in the discussion of the selection of nest-site variables. We tested for correlations between variables with Spearman's rank correlation, and found citrus type, inter-tree distance, and the number of limbs supporting the nest to be highly correlated with other variables. Thus, we eliminated them from further consideration. Statistical significance was set at $P \leq 0.05$ for all tests unless otherwise stated.

RESULTS AND DISCUSSION

Fifty-four nests representing five species were found in Grove 1, and 65 nests of seven species were discovered in Grove 2. Of these, the outcome was determined for 46 nests in Grove 1 and 39 nests in Grove 2 (Table 1). The most abundant nests were those of the Northern Cardinal, Brown Thrasher, and Common Ground-Dove, three of the most common species found in the Merritt Island citrus groves (Mitchell et al. 1995).

There are numerous potential predators in and around citrus groves, but Fish Crows (*Corvus ossifragus*) were probably responsible for most of the predation. They were seen near nests that had recently been depredated and were observed carrying nestling birds out of the groves on several occasions. Although otherwise intact, some depredated nests had their linings pulled up, which also lead us to suspect that crows lifted young out of nests. Snakes also were thought to be a significant source of nest loss. A yellow rat snake was seen at the base of a nest tree before our discovery that the nest had been recently depredated, and a yellow rat snake was found in another nest consuming nestlings.

Predation caused the loss of more than two-thirds of all nests in Grove 1 (Table 1). All other causes for nest failure accounted for 11% of the nests. Of the nests found in Grove 1, only 17% were successful. A greater percentage of the known nests was successful in Grove 2 (33%, Table 1). Predation also was responsible for most nest failures in Grove 2, but desertion and other causes accounted for nearly one-fifth of the nesting failures. Red-winged Blackbirds and Brown Thrashers suffered the greatest losses from predation in this grove. Fish Crows were thought to be responsible for four of five instances of predation on Red-winged Black-

TABLE 1

NESTING OUTCOMES (NUMBER OF NESTS) OF THE FIVE MOST COMMON BIRD SPECIES NESTING IN FLORIDA CITRUS GROVES IN SPRING 1989

Species	Total nests		Successful fledging		Predation		Desertion		Other causes of nest failure[a]	
	Gr 1	Gr 2	Gr 1	Gr 2	Gr 1	Gr 2	Gr 1	Gr 2	Gr 1	Gr 2
Common Ground-Dove	11	6	4	4	6	1	1	0	0	1
Brown Thrasher	13	15	0	4	11	9	1	2	1	0
Northern Mockingbird	4	2	0	1	3	0	1	0	0	1
Red-winged Blackbird	0	5	0	0	0	5	0	0	0	0
Northern Cardinal	18	11	4	4	13	4	0	0	1	3
All nests combined	46	39	8	13	33	19	3	2	2	5

[a] Includes deaths from pesticide exposure, starvation, sickness, injury, egg breakage, physical disturbance of the nest by heavy equipment, and unknown causes.

bird nests. The crows were seen either at or near the nest sites before we discovered the nest failures. Two of the thrasher nests were depredated when the citrus fruit was being picked. Because Fish Crows were sighted more often during or immediately after picking activity, we suspect that they caused the thrasher nest losses. We found that thrashers often gave distress calls when we were in the vicinity of their nests. The presence of fruit harvesters likely would have elicited distress calls from thrashers, facilitating the ability of crows to find nests.

The frequency of occurrence of successful and unsuccessful nesting outcomes in the two groves did not differ significantly for Common Ground-Doves ($\chi^2 = 2.4$, df = 2), but it did differ significantly for Brown Thrashers ($\chi^2 = 4.1$), Northern Cardinals ($\chi^2 = 4.4$), and for all species combined ($\chi^2 = 7.6$).

Daily nest survival rates were similar for all species in the egg stage, but varied widely in the nestling stage (Table 2). Brown Thrashers in Grove 1 had the lowest daily nest survival rate for nestlings. Interval survival rates were higher during the egg stage than the nestling stage for Brown Thrashers and Northern Cardinals, but not for Common Ground-Doves. Ground-dove nestlings had a much smaller chance of being destroyed than did the eggs. Nest survival rates spanning both the egg and nestling intervals were greatest for Common Ground-Doves in both groves, followed by Northern Cardinals in Grove 2. Brown Thrashers had the lowest rate of survival, particularly in Grove 1. Survival spanning the entire nesting cycle was higher in Grove 2 than in Grove 1.

Our Mayfield estimates of nesting success for Brown Thrashers and Northern Cardinals in the citrus groves were lower than that reported from

TABLE 2

REPRODUCTIVE SUCCESS OF COMMON GROUND-DOVES, BROWN THRASHERS, AND NORTHERN CARDINALS IN FLORIDA CITRUS GROVES IN SPRING 1989

Species	Grove	Exposure days		Daily nest survival rate		Interval nest survival rate		Nest survival rate across egg and nestling stages
		Egg stage	Nestling stage	Egg stage	Nestling stage	Egg stage	Nestling stage	
Common Ground-Dove	1	118	104	0.915	0.981	0.32	0.81	0.25
	2	57	44	0.947	0.977	0.49	0.78	0.38
Brown Thrasher	1	210	87	0.919	0.736	0.26	0.03	<0.01
	2	281	151	0.947	0.894	0.42	0.29	0.12
Northern Cardinal	1	380	132	0.953	0.864	0.48	0.27	0.13
	2	101	97	0.960	0.887	0.54	0.34	0.18

other studies. Mayfield nesting success rates of 44% for Brown Thrashers (Murphy and Fleischer 1986) and 51% for Northern Cardinals (Booth 1980) have been reported. Information on Common Ground-Dove nesting success is scant, but all the young in seven nests located and monitored in a pine plantation survived to fledging (Landers and Buckner 1979).

The high failure rates of Brown Thrasher nests in both groves and of Northern Cardinal nests in Grove 1 attributed to predation may have resulted from our nest monitoring activities. Both species became vocal when field technicians were near the nest sites. Corvids have learned to associate human activity and the response of some nesting passerine species with the presence of active nests (Gottfried and Thompson 1978, Best, pers. obs.) and may have discovered more nests because of our presence. Prior experience with citrus fruit pickers that disturb nesting birds also may have conditioned the crows. Salathe (1987) found that crows that successfully depredated European Coot (*Fulica atra*) nests would extend their searching around the depredated nests, sometimes resulting in destruction of all nests in the area. He concluded that disturbance created by investigator nest monitoring activities affected crow behavior by revealing nests and providing positive reinforcement. When Common Ground-Doves were flushed from the nest, they did not vocalize but sometimes gave a broken wing display. Those doves that did not display were probably inconspicuous to predators. Those that feigned injury sometimes continued the behavior as far as several tree rows away from the nest, perhaps luring predators from the nest site. Although Common-Ground Dove eggs are white, the dense citrus tree canopies probably shielded unattended eggs from view from outside the tree canopy. Because Common Ground-Dove nests were small and often placed on thick

branches, they were more cryptic than the larger nests of Northern Cardinals and Brown Thrashers. These differences may have accounted for the greater nesting success of Common Ground-Doves.

Differences in nesting success between the groves may have resulted from differences in predator populations, human activities, or vegetation structure. Grove 1, where nests suffered higher predation rates, was in a residential area, whereas Grove 2 was within the Merritt Island National Wildlife Refuge where human disturbance may have been less. The vegetation also differed substantially between the two groves and may have influenced nest predation.

Citrus culture operations were largely responsible for differences in grove vegetation. Tree hedging, topping, and skirt pruning influenced the geometry of the tree canopies and the inter-canopy distance, whereas mowing and herbicide application controlled the amount of herbaceous cover. Because the two citrus groves were managed differently, intercanopy distance was greater ($t = -2.0$, $P = 0.05$) in Grove 2 [249.1 ± 223.1 cm ($\bar{x}$ ± SD)] than in Grove 1 (143.4 ± 130.0 cm). Coverage of herbaceous vegetation also was greater ($t = -2.8$, $P = 0.008$) in Grove 2 (44 ± 27%) than in Grove 1 (21 ± 30%), but the opposite was true for bare ground coverage [($t = 3.6$, $P = 0.001$) Grove 2: 10 ± 18% Grove 1: 40 ± 37%.] Less vegetative cover in Grove 1 may have resulted in decreased nest concealment. Although some investigators have found no correlation between nesting cover and nesting success (e.g., Reynolds 1981, Conner et al. 1986), Ehrhart and Conner (1986) reported a correlation between vegetative cover around the nest and nesting success, and Martin and Roper (1988) found predation to be greater around less well-concealed nests.

In addition to altering herbaceous and tree-canopy cover, citrus culture operations may have affected breeding birds by creating disturbances which may have increased nest desertion, particularly during nest building. We suspect this because at least two nests were deserted during construction because of our nest monitoring activities. Also, pesticides, herbicides, and fungicides were routinely applied in the groves and had the potential of poisoning adults and nestlings, resulting in decreased survival and nesting success.

The low nesting success of the breeding birds in the citrus groves suggests that their reproductive output could have been below the replacement level. Such "sink" populations have been documented in other agricultural environments (Rodenhouse and Best 1983, Frawley 1989, Bryan 1990). Low reproductive success per breeding attempt may be compensated for by the long breeding season in Florida. Common Ground-Doves are thought to breed year-round in Florida (Baynard 1909 in

Howell 1932, Landers and Buckner 1979). Northern Mockingbirds and Northern Cardinals nest from March through August (Woolfenden and Rohwer 1969), and Brown Thrashers nest from March through July.

In Grove 1, litter coverage was significantly greater around the nest trees of all species [dove: 55 ± 26% ($\bar{x}$ ± SD), thrasher: 57 ± 26%, mockingbird: 46 ± 24%, cardinal: 60 ± 22%] than in the grove in general (21 ± 25), whereas the coverage of bare ground was significantly less (dove: 23 ± 27%, thrasher: 19 ± 25%, mockingbird: 19 ± 25%, cardinal: 16 ± 19%, grove: 40 ± 37%). Litter and bare ground coverages around nest vicinities in Grove 2 did not differ significantly from the grove overall, but the coverage of herbaceous vegetation around Northern Mockingbird nests (71 ± 19%) was significantly greater than the representative samples of the grove (44 ± 27%). When all species were compared, Northern Mockingbird nest vicinities had significantly more herbaceous vegetation coverage (Table 3). Because Common Ground-Doves, Brown Thrashers, Northern Mockingbirds, and Northern Cardinals commonly forage on the ground (De Graaf et al. 1985), the coverages of herbaceous vegetation, litter, and bare ground may have been important in their selection of a nest vicinity.

Inter-canopy distance was significantly greater around Northern Mockingbird nest trees in Grove 1 (287 ± 135 cm) than in the grove in general (143 ± 130 cm) and was greater around the nest trees of Northern Mockingbirds than around nest trees of the other three species (Table 3). Likewise, the number of young trees or open spaces where a tree was missing near the nest tree, a measure of the openness of the nest vicinity, was greater around Northern Mockingbird nest sites than around nest sites of the other species (Table 3). Woolfenden and Rohwer (1969) described ideal Northern Mockingbird nesting habitat as areas of "spaced" trees and found that nests were usually located in the more sparsely wooded or open sections of their plots. Brown Thrasher nest sites in Grove 2 had significantly smaller inter-canopy distances (144 ± 104 cm) than did a representative sample of the grove (250 ± 223 cm), suggesting that thrashers chose sections of the grove with more closed tree canopies. Inter-canopy distances for Brown Thrasher nest sites were similar in both groves, and differed from those of both mockingbirds and cardinals (Table 3). Fischer (1980) found that Long-billed Thrasher (*Toxostoma longirostre*) nests often were placed in thickets with dense leaf canopies that provided excellent concealment.

Selection of the nest vicinity also may have been influenced by the grove edges because edge habitats may have been important foraging areas. Fichter (1959) concluded that the breeding density of Mourning

TABLE 3

HABITAT VARIABLES ($\bar{x} \pm$ SD) CHARACTERIZING NEST SITES[a]

Habitat variables	Common Ground-Dove	Brown Thrasher	Northern Mockingbird	Northern Cardinal
Nest vicinity				
Litter (%)	48 ± 28A	46 ± 30AB	38 ± 25ABC	46 ± 28ABC
Bare ground (%)	20 ± 26A	14 ± 23AB	11 ± 21ABC	16 ± 25ABC
Herbaceous vegetation (%)	22 ± 28A	30 ± 32AB	44 ± 34C	29 ± 30AB
Herbaceous vegetation height (cm)	31 ± 20A	42 ± 27AB	53 ± 21BC	33 ± 20AB
Inter-canopy distance (cm)	179 ± 83A	143 ± 100AB	365 ± 142C	201 ± 121A
Openness near nest tree	1.6 ± 2.3A	1.5 ± 2.0AB	6.0 ± 2.9C	1.7 ± 2.1AB
Nest tree				
Canopy diameter (cm)	518 ± 111A	555 ± 106AB	369 ± 163C	493 ± 138A
Openness of tree canopy (%)	57 ± 28A	61 ± 21AB	55 ± 26ABC	46 ± 26AC
Tree height (cm)	427 ± 81A	476 ± 95B	392 ± 98AC	437 ± 139ABC
Nest placement				
Limb angle (°)	28 ± 30A	35 ± 30AB	69 ± 28C	38 ± 31AB
Limb diameter (cm)	4.4 ± 3.9A	1.8 ± 0.8B	1.5 ± 0.6ABC	1.5 ± 1.6BC
Foliage density above nest[b]	2.5 ± 0.6A	2.3 ± 0.6AB	2.3 ± 0.8ABC	2.3 ± 0.7ABC
Foliage density below nest[b]	1.2 ± 0.5A	1.5 ± 0.6AB	1.9 ± 0.9BC	1.4 ± 0.7ABC
Nest height (cm)	207 ± 43A	297 ± 84B	227 ± 109AC	241 ± 85AC
Relative nest height (%)	49 ± 8A	61 ± 13B	56 ± 18ABC	58 ± 28ABC

[a] For each habitat variable, means not sharing the same letter differed significantly ($P \leq 0.05$) when compared with a series of Student's *t*-tests.
[b] Foliage density estimates: 1 = cover <25%, 2 = 25–75%, 3 = >75%.

Doves (*Zenaida macroura*) in Idaho apple orchards was not affected as much by nesting cover as it was by the adjacent habitat type.

Canopy diameter, which was negatively correlated (Spearman's rho = −0.595, $P < 0.001$, df = 106) with inter-canopy distance, was smallest for Northern Mockingbird nest trees (Table 3). Also, Northern Mockingbird nest tree canopy diameters in Grove 2 (228 ± 65 cm) were significantly smaller than canopy diameters in the grove overall (528 ± 156 cm).

The openness of the nest-tree canopy was smallest for Northern Cardinals and differed significantly from Brown Thrashers (Table 3). Brown Thrashers chose the tallest trees for nest placement, whereas Northern Mockingbirds tended to place their nests in the shortest trees. When all species were compared, Brown Thrasher nest tree heights differed significantly from those of Common Ground-Doves and Northern Mockingbirds (Table 3).

Angles of limbs supporting mockingbird nests were significantly larger than those of the other species (Table 3). Diameter of limbs supporting nests was similar for all species, except for ground-doves, which had nests supported by larger limbs.

Relative nest height was greatest for Brown Thrashers and smallest for Common Ground-Doves (Table 3). When all species were compared, these two were significantly different from each other.

When successful and unsuccessful nests were compared for each species, only six of the nest site variables seemed to be related to nesting success. The nest vicinity and the placement of the nest in the tree were important, but the nest tree variables did not seem to be. In Grove 1, openness near the nest tree was greater for failed Northern Cardinal nests [1.7 ± 0.9 ($\bar{x}$ ± SD)] than for successful ones (0.5 ± 0.6). Nest concealment is believed to have a large influence on Northern Cardinal success (Ehrhart and Conner 1986), and an open nest vicinity may have facilitated Fish Crows in detecting activity around the nest site. In Grove 2, the height of herbaceous vegetation in the vicinity of Northern Cardinal nests was significantly less for successful nests (33 ± 10 cm) than for unsuccessful nests (55 ± 10 cm), but we have no explanation for this finding. Successful Common Ground-Dove nests in Grove 2 were placed in trees with significantly larger inter-canopy distances (267 ± 28 cm) than were unsuccessful nests (141 ± 51 cm), but we cannot explain this pattern.

Nest placement seemed to affect only Common Ground-Dove nesting success. Successful Common Ground-Dove nests in Grove 2 had supporting limbs with significantly smaller angles (10 ± 17°) than did unsuccessful nests (50 ± 17°). Because Common Ground-Doves build frail

nests with shallow depressions (Howell 1932), they may have chosen smaller-angled limbs for added nest stability. Mourning Doves preferentially place their nests on flat, horizontal limbs (Harris et al. 1963, Knight et al. 1984). Successful Common Ground-Dove nests in Grove 2 also were significantly closer to the ground (180 ± 12 cm) than unsuccessful ones (260 ± 34 cm).

Citrus groves seemed to be suitable breeding habitat for songbirds and doves, based on the number of active nests. Birds seemed to be making choices about the openness of the nest vicinity, the diameter and openness of the tree canopy, tree height, limb angle and diameter, and nest height. These choices may have been based on nest concealment and nest support, but did not necessarily influence nesting outcome. For example, the selection of nest trees with closed canopies did not seem to affect nesting outcome of Brown Thrashers, whereas the choice of small-angled limbs may have increased nesting success for Common Ground-Doves. Because citrus groves are unnatural environments subjected to periodic human disturbances which may inflate predation levels, the choices of some nest site characteristics that are adaptive in natural habitats may be neutral or even maladaptive in citrus groves.

ACKNOWLEDGMENTS

We are indebted to Margaret Dexter, Bret Giesler, and Patrick Carroll for their assistance in the field work. Brooks Humphreys of NASA provided access to the citrus groves on Merritt Island and taught us about citrus culture. This manuscript benefitted from reviews by J. J. Dinsmore, F. E. Lohrer, and T. E. O'Meara. Funding for this work was provided by Mobay Corporation. This is Journal Paper No. J-16470 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Project No. 3300.

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Wilson Bull., 108(3), 1996, pp. 584–588

SHORT COMMUNICATIONS

Exponential population growth of Monk Parakeets in the United States.—In the United States, at least nine species of introduced parrots now have established breeding populations (Lever 1987). The most abundant of these is the Monk Parakeet (*Myiopsitta monachus*). The exact date at which Monk Parakeets established breeding colonies in the United States is unclear because of uncertainty over when and where birds were released or escaped. The first confirmed sighting was in 1967 in New York City (Lever 1987), and the species was breeding there shortly thereafter (Bull 1973). By the early 1970s, the species was so widespread that the United States Fish and Wildlife Service (USFWS) initiated a control and removal program on the basis of the species' reputation in South America as an agricultural pest (Bump 1971, Bucher et al. 1992). By 1975, the year this program ended, the population of parakeets had been reduced by approximately one-half (Neidermyer and Hickey 1977). Since then, the numbers of Monk Parakeets have increased and the species has begun a dramatic population expansion to levels far above the pre-control numbers in the early 1970s. In this paper we document and analyze population trends of the Monk Parakeet in the United States from 1972 to the present.

Methods.—We summarized Christmas Bird Count (CBC) records published in "American Birds" (now "Field Notes"), personal communications solicited from bird watchers and ornithologists, and a continuing study of Monk Parakeets in Hyde Park, Chicago, that was initiated in 1992 (Hyman and Pruett-Jones 1995, Van Bael and Pruett-Jones pers. obs.).

We summarized CBC records from the 1971–1972 count to the 1994–1995 count. In examining these data for the 1972–1973, 1981–1982, 1986–1987, 1992–1993, and 1994–1995 counts, we checked records for every reporting locality in the contiguous United States. For the intervening years, we checked records for every locality within all states that reported at least one Monk Parakeet during at least one of the five counts listed above. For each CBC locality, we noted the total number of birds reported as well as the number of party hours. The regional reports were checked each year. For some years, Monk Parakeets were recorded during the "count week" at a given locality and mentioned in the regional summaries, but no birds were actually observed on the formal count day. In tabulating numbers of individuals recorded, we counted "count week" records as one parakeet at that given locality.

To calculate the rate of population growth, we used the standard equation defining exponential growth $N_{t+1} = N_t e^r$ where N_{t+1} is the population size at time t+1, N_t is the population size at time t, r is the rate of population growth, t is the time interval, and e is the natural logarithm base. This equation can be rewritten as $r = (\ln N_{t+1} - \ln N_t)/t$. We calculated r for each one-year time interval beginning in 1975 (the year the USFWS control program ended). A plot of r versus population size indicates whether a population is expanding, declining, or has reached a stable equilibrium size. The equation above defining r can be rewritten as $t = \ln 2/r$ to calculate the time interval for a population to double in size.

Results.—The Monk Parakeet was already widely distributed in the United States by the early 1970s. This appears to have been the result of geographically separated releases and escapes of captive birds (Neidermyer and Hickey 1977). The USFWS control program reduced the population size very successfully. This reduction is indicated both by the published records of the USFWS (Neidermyer and Hickey 1977) and by CBC records. At the start of the control program, birds were reported from 21 localities in seven states on the

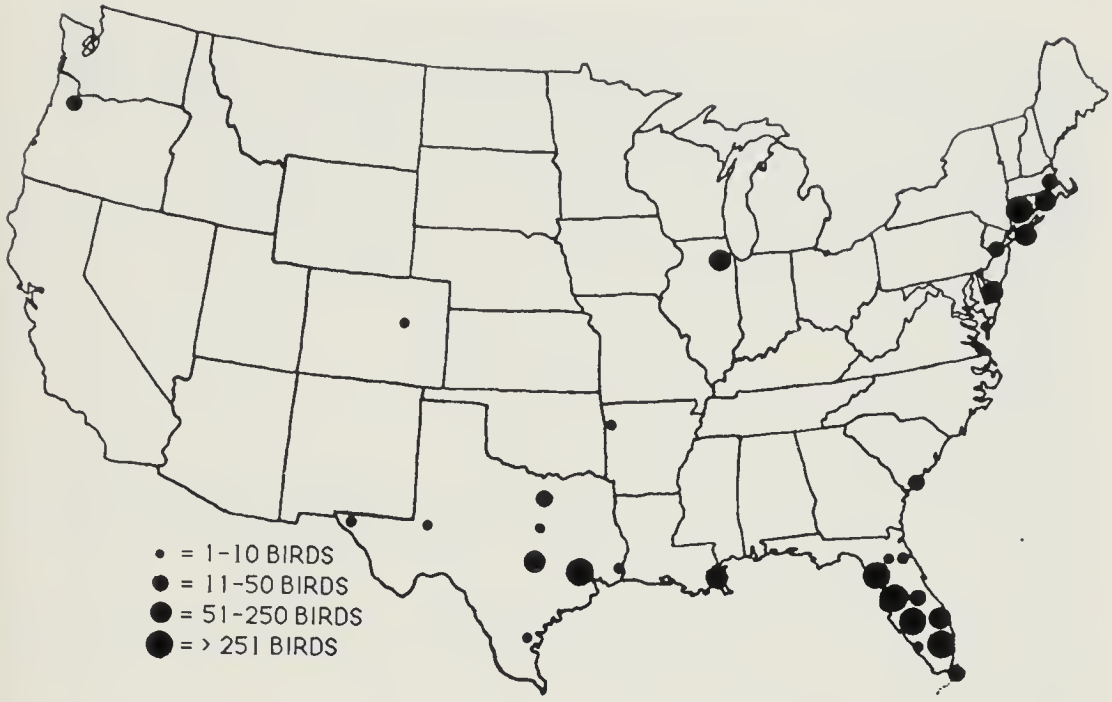

FIG. 1. Distribution and relative abundance of Monk Parakeets in the contiguous United States during the last five years as indicated by records from Christmas Bird Counts and unpublished observations.

1972–1973 CBC. Three years later, this was down to seven localities in five states (1975–1976 CBC).

Since 1975, the number of states and localities at which Monk Parakeets have been reported and the total number of individuals counted have all increased. Over the last five years (since the 1990–1991 CBC), the species has been reported from 76 localities in 15 states (Fig. 1). This includes 62 localities in 13 states from CBC records and regional summaries and an additional 14 localities in two states from personal communications to us from ornithologists. The population increase has been dramatic; on CBCs, 1816 birds were counted in 1994–1995 compared to 33 birds in 1975–1976. Monk Parakeets are not, however, evenly distributed across the United States. Two states, Florida and Texas, accounted for 1463 (80.6%) of the birds recorded on the 1994–1995 count (see Fig. 1).

The increase in numbers of Monk Parakeets fits an exponential model of population growth (Fig. 2). Regression of number of individuals recorded per party hour of effort (ln) by year from 1975 to 1995 is linear and statistically significant (Fig. 2, $F = 188.94$, $R^2 = 0.908$, df = 19, $P = 0.0001$). The average annual rate of population growth (r) equals 14.6% (N = 19, range = −58 − 76%), yielding a population doubling time of 4.8 years. A plot of population growth rate as a function of population size (Fig. 3) shows considerable fluctuation, but there is not yet any indication that the population is approaching an equilibrium level. The geographical range of Monk Parakeets has also increased since 1975. A plot of the number of CBC localities (ln) reporting the species since 1975 is linear and statistically significant ($F = 123.01$, $R^2 = 0.865$, df = 19, $P = 0.0001$).

In Hyde Park, Chicago, the population of Monk Parakeets increased from 64 in 1992 to 95 in 1993 (see Hyman and Pruett-Jones 1995). The population was not censused in 1994, but in 1995 we counted a minimum of 85 nesting chambers, indicating a population size of approximately 170 adults. This population has almost tripled in three years.

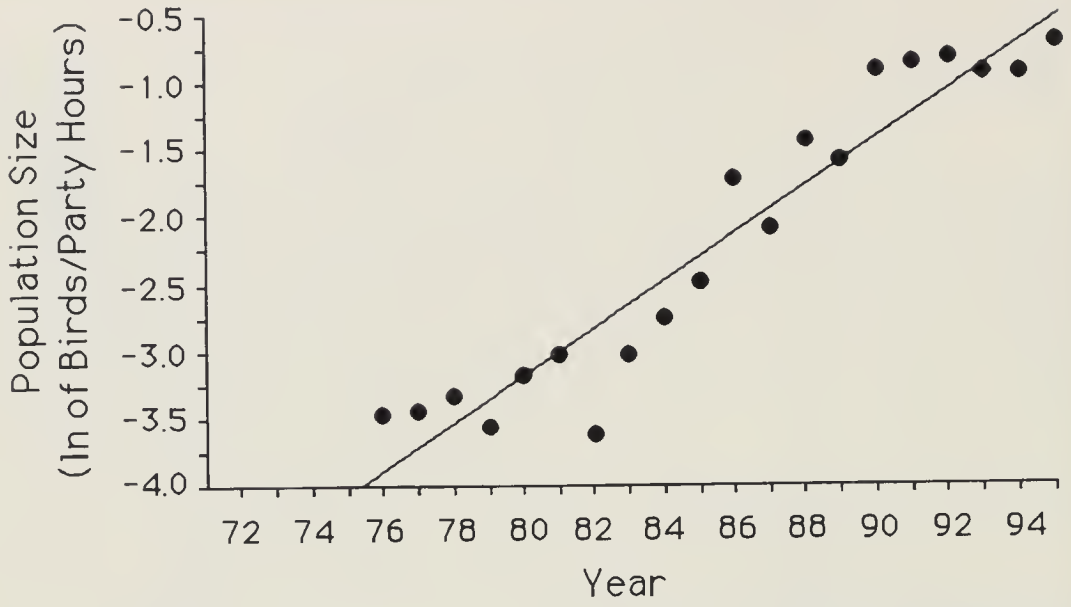

FIG. 2. Regression of total number (ln) of Monk Parakeets recorded on Christmas Bird Counts in the contiguous United States each year since 1975.

Discussion.—Our analysis shows that the Monk Parakeet is currently experiencing exponential growth in both its population size and geographical range in the United States. There is evidence to suggest that this increase is due to reproduction within existing populations rather than an increase in observer effort on CBCs or continued releases. First, the number of states reporting parakeets has remained relatively stable for the last ten years, fluctuating from five to nine. The increase in localities reporting parakeets has come from additional localities in those states already reporting the species. This suggests that the

FIG. 3. Plot of annual rate of population growth of Monk Parakeets in the contiguous United States for the period 1975–1994.

populations in those states are increasing and expanding into new areas. Second, of the 1816 individuals counted on the 1994–1995 CBC, 1253 (69%) were in localities which have had populations of Monk Parakeets continuously for the last eight to 10 years. At most of these localities, the numbers of parakeets reported has increased steadily over this time period. Finally, a known population in Hyde Park, Chicago, has experienced a dramatic increase in recent years believed to be entirely due to local production and recruitment of offspring. If other populations of parakeets are as productive as the birds in Hyde Park, Chicago, the nationwide pattern of exponential population growth can easily be explained. Although accidental or purposeful releases of Monk Parakeets probably continue, we consider it unlikely that these contribute to or explain their population growth.

The total population of Monk Parakeets is obviously much larger than indicated by the CBCs. In order to estimate the total population size, we need values of two parameters: the proportion of breeding populations of parakeets that are covered by the CBC count circles and the proportion of birds resident in the count circles that are actually recorded. As indicated in Results, over the last five years, Monk Parakeets have been recorded at 76 localities in 15 states. The CBCs comprised 49 (64.5%) of these localities. We can use this value (0.645) to estimate the proportion of parakeet populations that are covered by the CBCs. The second parameter, the proportion of resident birds that are actually counted is much more difficult to estimate. Unfortunately, there are no CBC localities reporting Monk Parakeets for which separate censuses of parakeets are also available. For example, in Hyde Park, Chicago, our census data are from an area not included in any of the Chicago CBC count circles. Without actual data, we cannot estimate this second parameter. If, hypothetically, the CBCs counted an average of half of the parakeets actually present in any one count circle, we can calculate what we consider to be a very conservative estimate of the total population as $1816/(0.645 \times 0.50) = 5631$. If, in contrast, the CBCs counted only an average of 10% of the parakeets in an area, the estimate would be $1816(0.645 \times 0.10) = 28{,}155$. The large range in these values illustrates how important census data will be to accurately estimate total population size.

Unless some decision is made to control the population of Monk Parakeets, it seems likely that the species will continue its range expansion and population increase in North America. As indicated by the success of the USFWS control program, the species is relatively easy to control through eradication of birds at their colonial nests. Nevertheless, the social and ethical issues associated with eradicating parakeets have lately proven much more difficult than the practical issues (cf. Temple 1992). In Hyde Park, Chicago, for example, a decision by the United States Dept. of Agriculture in the mid-1980s to remove the birds resulted in the formation of a citizen's action group to protect the parakeets and a threatened lawsuit. At present, it appears that in many areas the novelty of having a resident parrot species and concerns over animal welfare outweigh potential risks of the birds' becoming a threat to agriculture. Because Monk Parakeets may have that potential, continued monitoring of their populations and initiation of more detailed studies seems warranted.

Acknowledgments.—We thank the numerous individuals that shared their observations of Monk Parakeets with us, M. Pruett-Jones, D. Lanning, and two anonymous reviewers for helpful comments on the manuscript, and Dept. of Ecology and Evolution, Univ. of Chicago, and National Science Foundation for support.

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Wilson Bull., 108(3), 1996, pp. 588–591

Forest gap use by breeding Black-throated Green Warblers.—Habitat heterogeneity results from environmental gradients and disturbances that create spatiotemporal patchiness (White and Pickett 1985). Fine-grained patchiness resulting from forest gaps is a condition common in temperate forests (Blake and Hoppes 1986) and is typically caused by one to several tree-falls or tree death (snag) ranging in area from 0.0025 ha to about 0.1 ha (see Lorimer 1989). The resulting heterogeneity represents a habitat mosaic important to many species.

While collecting data on the foraging behavior of Black-throated Green Warblers (*Dendroica virens*) along the northern shoreline of Lake Huron in Michigan's eastern Upper Peninsula, we quantified breeding bird use of forest gaps. Data were collected from 14 June through 19 July 1994. Transects were established parallel to the Lake Huron shoreline at distances of 0.4 km (0.25 mile), 0.8 km (0.5 mile), 1.6 km (1.0 mile) and 3.2 km (2.0 mile). Observers followed these transects for a distance of 6.4 km (4.0 mile), collecting observations on males (and females if possible) at each established territory (determined by the presence of a singing male). Because birds were territorial, only one observation per sex was made at any location. A minimum distance of 100 meters between observations was established to ensure the independence of data collected (Heijl and Verner 1990).

We used Brokaw's definition of a forest gap—a hole (minimum of 5 m in diameter) in the forest canopy extending through all levels down to an average height of two meters above ground (Brokaw 1982). A bird was considered to be using a gap if it was observed foraging or singing within 1 m of the canopy edge. We did not count transients—birds flying through the gap or otherwise obviously not using the gap to obtain food or as a territorial boundary.

Forest vegetation in the study area consisted of a mixture of conifers including balsam fir (*Abies balsamea*), northern white cedar (*Thuja occidentalis*), white spruce (*Picea glauca*), eastern white pine (*Pinus strobus*) and deciduous species including paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*) and red maple (*Acer rubrum*). Mature canopy was approximately 13.5 m with an understory principally of balsam fir and white spruce.

Observations within 50 m of roads, open fields or the Lake Huron shoreline were not

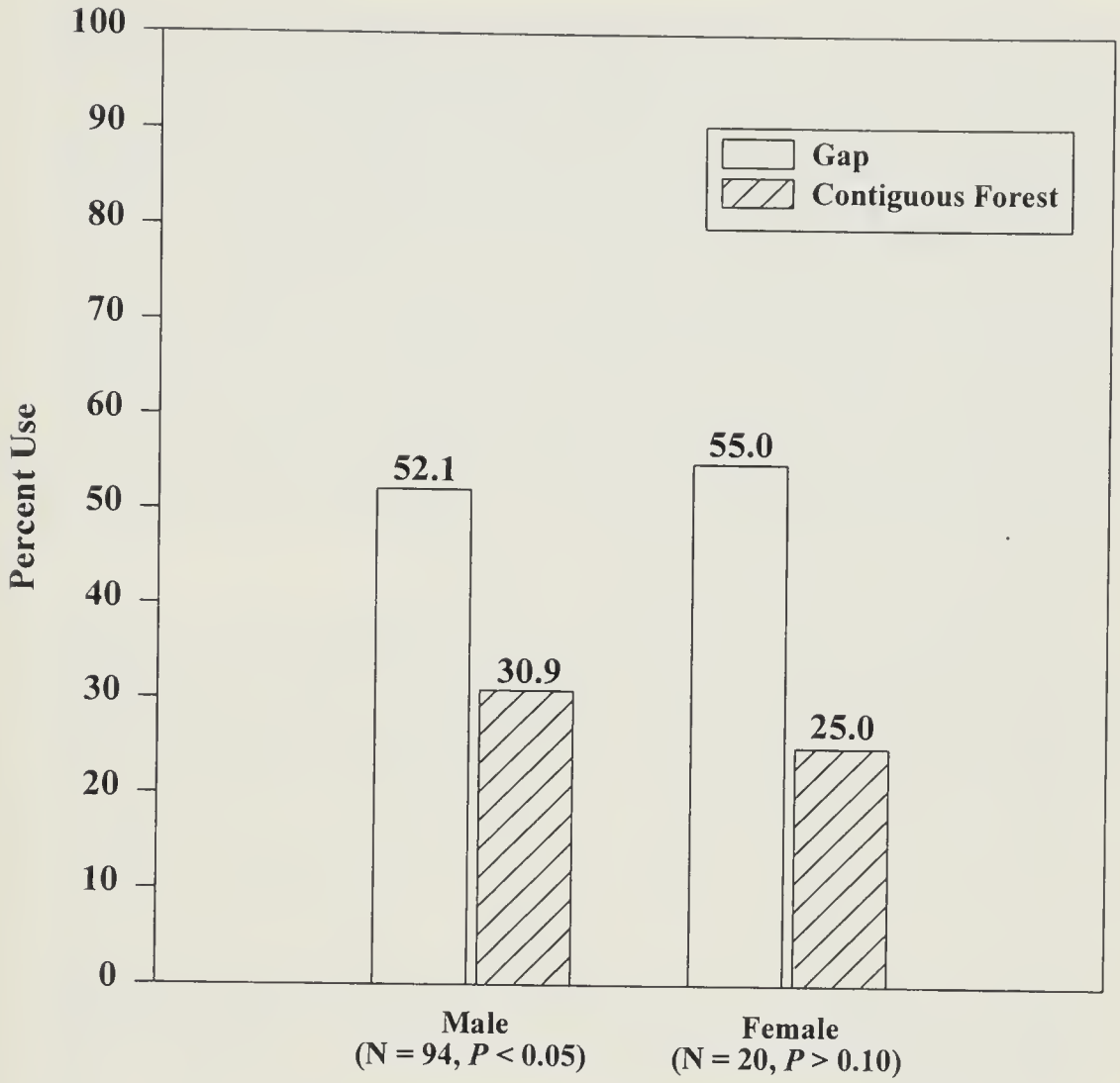

FIG. 1. Breeding Black-throated Green Warbler gap usage, 1994.

included in the statistical analysis in an effort to reduce possible bias due to edge effect. We used log-likelihood ratio G tests to analyze for differences in gap use by breeding birds (Zar 1984). As we did not measure gap area, we were unable to base our expected values on relative area of gaps versus contiguous forest. Thus, we were conservative in our calculation of expected values, assuming a 1:1 ratio of gap use to forest use.

During the breeding season, males were observed utilizing forest gaps significantly more and contiguous forest significantly less than expected ($G = 5.19$, $P < 0.05$; Fig. 1). Males were observed in, or immediately adjacent to, tree-fall forest gaps in 52.1% of our observations and in contiguous forest in 30.9% of our observations (N = 94). Females demonstrated an even greater difference in use, utilizing gaps 55.0% of the time and contiguous forest 25.0%, however, this was not significant ($G = 2.31$, $P > 0.10$) (Fig. 1). This lack of significance may be the result of low statistical power due to small female sample size (N = 20).

These observations, though potentially limited in that data were from only one breeding season, indicate the potential importance of gaps to breeding birds. Gaps may be important to breeding birds for a variety of reasons. For instance, foliage insectivores such as the

Black-throated Green Warbler may select preferentially gaps in response to differential prey abundance. There may be more insects in gaps due to greater primary productivity associated with higher light levels (Fogden 1972, Blake and Hoppes 1986). Previous work has demonstrated differences in assemblages of birds captured in gaps and the surrounding understory (Blake and Hoppes 1986, Martin and Karr 1986, McGowan-Stinski, pers. comm.). These differences have been correlated to an increased insect, fruit, and total foliage abundance in forest gaps (Blake and Hoppes 1986, Martin and Karr 1986).

The increased light penetration in forest gaps (Fogden 1972, Blake and Hoppes 1986), may result in warmer microclimates in gaps as compared to contiguous forest. Warmer microhabitats could benefit the thermoregulatory physiology of insects, increasing insect activity and abundance. Birds may thus be attracted to this activity and/or abundance as they attempt to increase foraging opportunities. Additionally, warmer temperatures within a gap may benefit a bird as it attempts to budget energy and deal with exigencies faced during the early breeding season such as cold mornings. Thus, gap foraging may be energetically advantageous through providing a bird with a concentrated source of prey, as well as a reducing an individual's thermoregulatory costs, allowing birds to shunt more energy into the breeding effort and less into individual maintenance.

The vegetation structure of forest gaps may help birds maximize their foraging profitability. Because gaps typically have a lower vegetation profile as well as a higher density of foliage (see Martin and Karr 1986), gaps may present birds with a more compact area to visually search and move about in. Increases in foliage density may yield more insect prey per unit of search time and reduce an individual's energetic expense in movement. High foliage density in gaps may also reduce a foraging bird's vulnerability to predators.

Finally, anecdotal evidence suggests forest gaps may aid males in establishment and maintenance of territorial boundaries. Black-throated Green males typically spend much of their time defending territory through visible and acoustical advertisement (Morse 1993). Utilization of a forest gap, especially a younger gap, as a territorial boundary may benefit males through increased visibility and song projection. We observed numerous aggressive male interactions occurring over or immediately adjacent to forest gaps by territorial males. Singing males were also observed responding to each other across gaps. This evidence suggests that at least some males at our study site may have been using forest gaps as territorial boundaries.

Our data suggest the importance of forest gaps to breeding Black-throated Green Warblers along the northern Lake Huron shoreline. This use suggests that structural heterogeneity in mature forest provides Black-throated Green Warblers with higher quality habitat than is found in less heterogeneous, more even-aged forest stands. A better understanding of the importance small scale disturbances play is critical if forest managers are to maintain high quality habitat for breeding resident and neotropical migrant birds.

Acknowledgments.—This project was funded in part by The Nature Conservancy—Michigan Chapter, Central Michigan Univ. Graduate School and Biology Dep., and the National Fish and Wildlife Foundation. We thank M. J. Hamas of Central Michigan Univ. and D. Ewert of the Michigan Chapter of the Nature Conservancy for assistance in the field as well as advice and support. The manuscript benefited from the comments of G. Kelley, T. Contreras, D. Cimprich and J. McGowan-Stinski.

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Wilson Bull., 108(3), 1996, pp. 591–592

Courtship behavior of Golden-cheeked Warblers.—The Golden-cheeked Warbler (*Dendroica chrysoparia*) is an endangered species with a known breeding range mostly confined to the Edwards Plateau of Texas. These warblers inhabit oak-juniper woodlands and are dependant on *Juniperus ashei* bark for nesting material (Sexton, Birding 24:373–376).

Pulich (1967, The Golden-cheeked Warbler, a Bioecological Study, Texas Parks and Wildlife) described courtship displays in Golden-cheeked Warblers in which males attentively followed females and briefly displayed before copulation. There are no other published accounts of this type of behavior in this species. Courtship behavior in Golden-cheeked Warblers was observed on two occasions during spring 1995. The following observations were made at Pedernales Falls State Park, Blanco Co., Texas on 27 March 1995 and at Colorado Bend State Park, San Saba Co., Texas on 4 April 1995. In both cases, a female Golden-cheeked Warbler was discovered constructing the base platform of a nest prior to the observations of courtship behavior. The female warbler would make short forays into neighboring *Juniperus ashei* to collect strips of bark. All of the nesting material gathered during these observations was from trees within 15 m of the nest tree. The nest at Pedernales Falls was 5.3 m high in *J. ashei,* and the nest at Colorado Bend was 4.7 m high in *Ulmus crassifolia.* While observing the female's activities, a quiet, warbler-like song was heard that was unlike either of the primary songs of the Golden-cheeked Warbler (Pulich 1976). This song was muted, but more rapidly paced, than the typical songs of the species. This combination gave the song a more twittery quality than the primary songs. However, despite these differences, the song had tonal qualities similar to the other songs of the species. The

male warbler was observed singing this song in trees near the nest. He sang for two to three minutes during which the female continued nest construction; no change in her behavior was noticed. The male stopped singing as he approached the nest site. On both occasions the male was carrying strips of juniper bark. The bark was given to the female. The female then placed bark strips in the nest. While the female was placing the bark, the male quietly sang the twittery song and spread his tail while slowly lowering and flicking his wings closed. When the female finished placing the bark strips, she faced the male, quietly chipped, and crouched with her wings slightly spread and her head down. Similar behavior was noted in both cases. During the first observation, copulation occurred on the nest platform. The nest of the second pair was farther along in construction and the copulation occurred next to the nest. After copulation the male repeatedly sang the same twittery song while flying from perch to perch, widely circling the nest tree. During this time, the male constantly flitted its wings and fanned its tail. Tail and wing fanning are not limited to courtship displays; I have observed similar behavior in Golden-cheeked Warbler territorial interactions as well as toward Texas rat snakes (*Elaphe obsoleta lindheimeri*) and when a female Brown-headed Cowbird (*Mothrus ater*) was near the nest.

Nest building in Golden-cheeked Warblers is reported to be done entirely by the female (Pulich 1976, Oberholser, 1976, The bird life of Texas, Univ. of Texas Press). During the early spring of 1994 and 1995 I observed males carrying nesting material on five occasions. Other workers also have observed male Golden-cheeked Warblers visiting nests under construction (Keddy-Hector, pers. commun.). This suggests that male warblers may have some role in nest construction.

These observations suggest that male Golden-cheeked Warblers carrying nesting material may have been part of courtship. This does not eliminate the possibility that, at least occasionally, the male may have a minor role in nest construction. However, no direct observations were made of males adding materials to a nest. In addition, no specific male was observed carrying nesting material on more than one occasion. During previous observations of male Golden-cheeked Warblers carrying nesting material, there was no evidence of a female in the vicinity and the twittery song that was given prior to and following the courtship behavior was not heard.

Acknowledgments.—I thank Dean Keddy-Hector for his input throughout the preparation of this manuscript. I also thank David Riskind, Leila Gass, Millicent S. Ficken, and C. R. Blem for their comments on earlier drafts of this manuscript.

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Wilson Bull., 108(3), 1996, pp. 593–601

ORNITHOLOGICAL LITERATURE

Edited by William E Davis, Jr.

The Northern Goshawk: ecology and management. By William M. Block, Michael L. Morrison, and M. Hildegard Reiser, editors. Studies in Avian Biology 16. Cooper Ornithological Society, % Western Foundation of Vertebrate Zoology, 439 Calle San Pablo, Camarillo, California. 1995: 34 figs., 58 tables. $16.00 (paper).—Honest-to-goodness updates of species' life-history information—as opposed to simple rehashings of previously published accounts—are always welcome additions to the ornithological literature. This is especially true when the species in question is one whose known biology is steeped as much in myth and traditional lore as ecological reality, and even more so when the information in question focuses on limiting-factors research at multiple sites. The current offering is one such effort. The published result of a symposium on the biology and management of the Northern Goshawk (*Accipiter gentilis*) that was held in conjunction with a Cooper Ornithological Society meeting in April, 1993, the work represents "a compendium of current information on goshawk biology and management" in North America.

The symposium was organized because evidence available at the time suggested that North American populations of goshawks, especially some of those in the western United States, were declining, and because resources managers had insufficient information upon which to base practical and effective management efforts. Although the former is no longer thought to be the case, the resulting proceedings remains a useful and timely contribution to the avian literature. The 22, 4- to 9-page papers that make up the work were authored or co-authored by an astounding 41 individuals, testimony to recent interest in the species. The work includes six contributions on "research approaches and management concepts," nine on "resource ecology," and seven on "population ecology." Not surprisingly, not all of the efforts included therein are as scientifically rigorous or as gracefully presented as one might hope. Several papers, for example, offer but brief and preliminary glimpses of works that were still in progress at the time. Nevertheless, the proceedings' editors are to be congratulated for producing a work that is both editorially clean and reasonably seamless.

Several of the more generically useful papers include ones by Clint Boal on aging nestling goshawks, and Suzanne Joy, Richard Reynolds, and Douglas Leslie on the costs of benefits of broadcast survey techniques for breeding goshawks. Although most "management" papers in the work are clearly aimed at site-specific situations, many of the conclusions reached should be of general interest to managers of forest raptors. A paper by Pat Kennedy, Johanna Ward, George Rinker, and Jim Gessaman on post-fledging areas in goshawk home ranges, for example, insightfully concludes that management strategies need to account for the habitat requirements of recently fledged young, as well as for the nest-site and foraging-area requirements of parental adults. Similar bits of wisdom occur in other papers.

Overall, the symposium offers a wealth of new information, as well as a good read. There is, however, one troubling aspect of the work on which I need to comment. Many of the management strategies laid out in the symposium are basically "product" rather than "process" driven (i.e., most managers still seem intent on maximizing local goshawk production—principally by creating species-specific, "designer habitats" for the species--rather than on trying to establish fully functional, naturally forested ecosystems typical of the regions in question). Given that the goshawk does not appear to be severely threatened in any major portion of its North American range, should we really be trying to maximize its production in managed forests. Wouldn't conservation interests be better served by trying to reestablish a full suite of natural ecosystem functions in "natural" forests. As I read most

of the management papers in the work, I couldn't help but wonder whether the use of silvicultural analogs alone (e.g., substitute "numbers of Northern Goshawk nestlings produced per year per" for "amount of softwood board feet per year") will ever really work in forest conservation and whether we need to be looking at management strategies that extend beyond the current single-species, production-oriented, paradigm.

This latter, not-so-minor, caveat notwithstanding, the current offering should be read by all who have an interest in the species, as well as by those with interests in the species' forested habitats. The Cooper Ornithological Society is to be congratulated for making the proceedings available so quickly, and at such a reasonable price.—KEITH L. BILDSTEIN

HOW BIRDS MIGRATE. By Paul Kerlinger, illus. by Pat Archer. Stackpole Books, Mechanicsburg, Pennsylvania 1995: 228 pp., 16 maps, 43 figures, 2 tables. $14.95 (paper).—The ornithological literature is full of books on bird migration. My own collection takes up more than a meter of shelf space, and the current offering represents Kerlinger's second addition to the group in less than a decade. Even so, "How birds migrate" provides an especially welcome and long-overdue complement to the existing literature. Indeed, not since Donald Griffin's classic work on the subject in 1964 (Bird migration, Doubleday, Garden City, New York) has anyone managed to distill and highlight the current ornithological literature on bird migration in such an appealing and productive fashion. Kerlinger's text, which contains little of the byzantine modeling, mathematics, and jargon of the current technical literature, retains all of its essential findings and excitement.

The work consists of 15 chapters, ranging from one on why birds migrate to one on how conservationists are attempting to protect them. There is also an especially useful annotated list of additional references. Most chapters focus on single aspects of migration, introducing and detailing their essential features and concluding with a series of case studies highlighting the phenomenon in individual species. The work is accompanied by an effective series of maps that depict the migratory pathways of species, as well as by numerous illustrations of specific aspects of migration behavior and ecology.

In his previous offering (1989, Flight strategies of migrating hawks, Univ. of Chicago Press, Chicago, Illinois), Paul Kerlinger demonstrated an extraordinary talent for summarizing the migration literature for his colleagues. His current effort demonstrates a similar talent for doing so for the much larger lay audience. In fact, Kerlinger sets an enviable standard for others who would try to do the same. The book's level of treatment, together with its modest price, make it an appropriate companion text for introductory courses in ornithology and avian ecology and behavior. "How birds migrate" should serve as a useful introduction to bird migration well into the next century.—KEITH L. BILDSTEIN

THE SUMMER ATLAS OF NORTH AMERICAN BIRDS. By Jeff Price, Sam Droege, and Amy Price. Academic Press, San Diego, California. 1995: 364 pp., 463 maps, 16 line drawings. $45 (cloth).—The stated goals of this book are to help birders find birds, and to provide information and guidance to conservation organizations and land managers. The book certainly reaches these goals. The data base of this book is the National Biological Survey's North American Breeding Bird Survey (BBS). The first chapter provides an overview of the BBS, including a discussion of the biases and constraints inherent in a survey which is confined to roadsides and in which most of the data is collected by amateur volunteers. Chapter 2

explains in detail how the BBS data was used to create the maps, and all the problems, biases, checking, and trouble shooting involved. The bulk of the book, chapter 3, consists of relative abundance maps, with a level of resolution of 50 km by 50 km blocks, for 450 species and identifiable forms of North American summer birds. Most of the maps show averages of data collected from hundreds of 1985–1991 BBS routes (50 three-minute point counts along a 40 km route) in southern Canada and the contiguous United States. Strictly speaking, the maps do not show breeding bird distribution because non-breeding birds may be represented. Each map has four levels of abundance displayed (<5, 5–20, 20–50, and >50 birds detected per route per year), with a minimum mapped value of 0.5. Unfortunately, the four levels are shown by different levels of intensity of the same color, which makes some maps difficult to read. Additional maps show species richness patterns for all species combined, and for several groups of birds (e.g., herons, waterfowl, flycatchers, warblers). Chapter 4 presents an annotated list of species of 531 species or forms. This includes the species for which there was insufficient data to create a map, and BBS data from Alaska and northern Canada. The annotations for each species include a description of habitat, and three BBS routes that have had consistently high counts for the species. For each route the information presented includes the average number of individuals per year detected, frequency (e.g., 7/7 indicates that the species was detected in all seven census runs from 1985–1991), and location. A fifth chapter addresses population trends and conservation issues. It includes an extensive table of population trends (percentage change), both long term (1966–1993) and short term (1984–1993), with levels of statistical significance for population changes indicated. The chapter includes a discussion and analysis of possible causes for population trends in several groups of birds (e.g., scrub nesters, open water and wetland species), keying mostly on habitat alteration. The four appendices include a list of scientific names, references cited and suggested readings, the American Birding Association's code of ethics, and selected birdfinding guides and breeding bird atlases for each state. The index includes only bird species. The 16 drawings by David D. Beadle add an attractive touch to what is essentially a book of maps.

I find this an interesting and useful presentation of BBS data which should have heuristic value, and recommend it to anyone interested in avian biogeography, conservation, or birdwatching.—William E. Davis, Jr.

The atlas of breeding birds of Connecticut. By Louis R. Bevier (ed.). Bulletin 113, State Geological and Natural History Survey of Connecticut, Dept. of Environmental Protection, Hartford. 1994: 461 pp., 184 maps, 190 line drawings. Available from: DEP-Publications, 79 Elm Street, Store-Level-MO, Hartford, CT 06106-5127 (checks payable to DEP-PUBLICATIONS). $36.95 plus $3 p&h (cloth).—Another in a series of state and province breeding bird atlases, this book provides baseline data for the breeding birds of Connecticut. These data should be useful both for future evaluations of natural and human-induced bird population changes and for immediate use in making informed decisions on conservation priorities by conservationists, legislators, and state agencies. Because of its relatively small size, all of the state was censused (larger states have used a priority block system), dividing the state into 121 7.5 minute quadrangles (USGS quadrangle system), each divided into 6 blocks of approximately 25 km^2 each. More than 500 individuals were involved in the data collection from 1982–1986. "Block busting" (a few observers spent a few hours) ensured at least some coverage for every block. Each species was assigned a breeding status of "Possible," "Probable," or "Confirmed" using suitable criteria and maps

for each species were compiled. Two hybrids and 173 species were in the confirmed category, including two species which had not been previously recorded breeding in Connecticut.

The book has an interesting design—24.5 cm wide, 20.4 cm tall—which makes for easy reading. The maps are large and particularly easy to read. Several sections deal with the limitations of the study (e.g., level of effort of data collection was neither uniform nor measurable) and there is an interesting 11 page section by George A. Clark, Jr. on interpreting the distribution of breeding birds (including associated problems and constraints). The bulk of the book is occupied by the species accounts. Each species which was either a confirmed or probable breeder is described in a two (facing) page section which includes an introductory statement, and habitat requirements, atlas results, and discussion sections. The introductory statements usually provide current status information (e.g., Threatened or Special Concern), and the discussion section generally concentrate on historical accounts and population trends. An attractive line drawing by Michael DiGiorgio accompanies each account. More succinct accounts are presented for possible breeding and miscellaneous species. One appendix summarizes the breeding status (e.g., number of blocks in which breeding was confirmed), a second presents Breeding Bird Survey population trends for Connecticut and southern New England, and a third a list of common and scientific names of plant and animal species (excluding birds) mentioned in the text. The Literature Cited section contains over 500 references and is a veritable goldmine for local references.

This is a generally excellent book, but is not without problems. I was sorry that the Monk Parakeet (*Myiopsitta monachus*) was not included in the data collection, since it has been a documented breeding species for years, and population changes in this species should be of future interest. The species accounts, although well done, are a bit thin, in many cases occupying less than a page of text. There is a lot of white space that might well have been usefully filled with descriptions of breeding-related behaviors such as nest building, courtship displays, foraging behavior during the breeding season, and care of the young. These are minor quibbles however—this is an important contribution to the breeding-bird literature of North America.—William E. Davis, Jr.

The West Virginia breeding bird atlas. By Albert R. Buckelew, Jr. and George A. Hall. Univ. Pittsburgh Press, Pittsburgh. 1994: 232 pp. plus acetate overlays, 173 distribution maps, 4 introductory tables and 12 figures. $27.95 (cloth).—With this attractive publication, West Virginia joins the ranks of at least 15 North American states and provinces that have published breeding bird atlases. In the present volume, more than 300 volunteers conducted field work between 1983 and 1989. The southeast corner of 7.5′ topographic maps was targeted as the priority block for most of the state. In addition to priority blocks, fieldwork was conducted in blocks with special features, volunteers' "favorite" areas, and locations covered by Brooks Bird Club field trips. Of the potential 2,700 blocks in the state, 516 were targeted by the study. A total of 171 species is mapped.

The introduction provides background on West Virginia's atlas effort, methods, and organization. It also includes a brief overview of biogeography, physical features, and climate of the state that may influence bird distribution. Maps that display physiographic features are presented here and as seven acetate overlays. Because the state's avifaunal regions and habitat types are nicely described and illustrated by Hall ("West Virginia Birds," 1983), they are not duplicated in the present volume. Project results are disappointingly slim, with little reference to survey effort. No indication of the number of hours of fieldwork, for

example, is presented, and the exact number of blocks surveyed is not clear. Survey effort seems comparable to most other atlases, although the authors state that coverage was not even. Highlights include first breeding records in West Virginia for the Yellow-bellied Flycatcher (*Empidonax flaviventris*) and Yellow-rumped Warbler (*Dendroica coronata*). Other northern species, such as Veery (*Catharus fuscescens*) and Dark-eyed Junco (*Junco hymenalis*), were documented farther south in the western hills than expected.

Like many other states, West Virginia used a priority block system to promote uniform coverage. However, the inclusion of nonrandom blocks has the risk of accentuating coverage inconsistency. Opportunistic coverage of blocks selected by volunteers, notably in the Canaan Valley (Blackwater Falls quadrangle), creates an awkward cluster of observations for common species, such as Common Yellowthroat (*Geothlypis trichas*). This problem was avoided in "The Atlas of Breeding Bird of Michigan" (R. Brewer, G. A. McPeek, and R. J. Adams, Jr.; 1991) by mapping results at a coarser scale than data were collected.

Species accounts are concise, incorporating the atlas map, text, and a tabular summary on a single page. Four map symbols are used to reflect the levels of breeding evidence. "Observed" records are mapped, even though those records are defined as indicating no evidence of breeding. The map symbols are not, to my eye, intuitively hierarchial, but have the advantage of being clearly distinguishable. The base map includes state counties and a grid of topographic maps, creating a busy map. The topographic grid, and corresponding key in the appendix, makes this one of the easiest atlases in which to pinpoint the location of records. The accounts are generally free of typographical errors and are well edited. They provide a concise summary of habitat, distribution, historical patterns, and population trends. An appendix discusses the status of eight species not confirmed during the atlas efforts. The literature cited is surprisingly brief and reflects frequent reference to Hall's previous volume. The index includes both English and scientific names.

West Virginia has contributed a useful addition to the growing collection of published breeding bird atlases, targeted well to local interests. I recommend it to students of bird distribution in the region.—Daniel W. Brauning.

A bird-finding guide to Ontario. Revised Edition. By Clive E. Goodwin. University of Toronto Press, Toronto. 1995: 477 pp., 41 maps. $24.95 (paper).—This revised edition updates the information in the 1982 edition and provides more information on the status of individual species. The task of providing a bird-finding guide to an area so large and ecologically diverse is enormous—Ontario has an area of over one million km^2 with deciduous and boreal forest, tundra, farmland and prairie, and a vast shoreline along the Great Lakes. It takes five pages to tell you how to use the book (this includes, however, an excellent section on birding ethics). Chapter 2 introduces the reader to the diversity of habitats and the birds found in each, as well as a discussion of seasonal variations. Chapters 3–16 are site guides for individual or clusters of counties in southern Ontario, while chapters 18 and 19 deal with the vast regions of northern Ontario. The chapters start with an overview which generally includes topography, flora, birding possibilities, and weather and seasonal changes. The distances are in kilometers, and direction usually given to the nearest tenth of a kilometer, which is excellent. The maps need to be supplemented by provincial road maps, however. The coverage of the areas of Ontario I know best (e.g., Algonquin Park) were adequate but lacked the detail of the American Birding Association birdfinding guide series. Much useful information, e.g., the Wolfe Island ferry schedule, is included, however. Chapter 19 deals with useful information for the visitor such as accommodations, hot line telephone

numbers, and important reference books. Chapter 20 is a systematic list of the birds, with text and bar graphs for each species. An appendix provides common and scientific names for the mammals, reptiles, and plants mentioned. The index is extensive and printed in the same type size as the text which makes it easy to read.

The book is generally well written, although a stronger editorial hand could smoothed out such statements as, "Fifteen species of ducks have been proved to nest. . . ," and in my copy page 344 was missing completely. A few of the maps lack scale bars so distances are hard to judge. The book won't fit into your pocket but will fit into your glove compartment. It is a bit overwhelming because of its scope and complexity, but next time I go to Ontario I will certainly take my copy along.—William E. Davis, Jr.

Birdfinder: a birder's guide to planning North American trips. By Jerry A. Cooper. American Birding Association, Inc., Colorado Springs, Colorado. 1995: 374 pp., 40 maps, 22 line drawings. $17.95 (wire-o binding, stiff paper).—This latest addition to the American Birding Association's (ABA) "Birder's Guide" series is in the same format with a wrap-around rear cover which can act as a book mark and protects the pages. It differs from previous guides in its scope and intent—it is primarily a trip planner—and should be used in conjunction with local bird finding guides. The first 19 chapters outline 19 trips, in chronological order so that they all could be taken in a single year, which theoretically might allow a birder to see 650 species of birds in North America. An additional "Baker's dozen" trips would allow the birder to add a few species to that list. In fairness, list-building is not the entire focus of this guide—quality of experiences is also emphasized. The chapters present general itineraries (including map or maps) for the trips scattered about Alaska, the contiguous 48 states, and Canada, timed at the best season for birds. They also present a plethora of details on trip planning, including a list of birding guides, telephone numbers and addresses for outfits which offer special services (e.g., pelagic trips), rare bird alert telephone numbers, a list of key species that should be looked for, tips on accommodations, and budget guidelines. A final chapter entitled "The Birdfinder Chart," which occupies more than 50 pages, lists the entire ABA checklist of species and indicates on which trips each is a key, probable, possible, or remotely possible species. This list also functions as the index to species for the guide—the actual index does not include bird names.

As is typical of the ABA guides, the book is sturdy, easy to read, and well designed. There are a few typos (mostly words run together) but it is generally well edited. This guide should be useful to the birder looking for adventure or to the more serious bird student who might want to have a look around before or after a professional conference. It is loaded with useful tidbits of information and is certainly worth the money.—William E. Davis, Jr.

Edward Lear: a biography by Peter Levi, Scribner, New York, 1995, 363 pp, 41 black-and-white illustrations, 2 appendices, bibliography, $30 (cloth).—The English poet, painter, and travel-writer, Edward Lear (1812–1888), of Lear's Macaw fame, is best remembered today for a single child's verse in which an improbable pair of characters take to sea "in a beautiful pea-green boat," court, marry, and "dance by the light of the moon." "The Owl and the Pussycat," written in 1867, was a relatively late addition to the hundreds of songs, poems, limericks, and "nonsense" rhymes Lear created for the enjoyment of his friends' young children. When he published them for a much larger audience, beginning in 1846,

these flights of fancy proved an unexpected commercial success and established Lear as one of the most beloved children's writers of all time.

It is no coincidence that "The Owl and the Pussycat" and so many of Lear's other stories feature birds, for the author/artist began his professional career by painting exotic birds at the London Zoo. By the age of 20, he had published a spectacular monograph on parrots ("Illustrations of the Family of Psittacidae or Parrots," 1832) and was providing ornithological illustrations for many of the most influential British ornithologists of his day, including Prideaux John Selby, William Jardine, T. C. Eyton, and John Gould. His work was favorably compared with Audubon's, and he was, in the mid-1830s, poised at the start of a career that might have made him the most successful wildlife artist of the 19th century. How he reached that point, and why he gave it up to pursue a less illustrious life as a poet, writer, and landscape painter, are among the many interesting aspects of Edward Lear's life inadequately addressed in Peter Levi's new biography.

In his introduction, Levi, a poet and literary historian with several previous biographies to his credit (including books on Shakespeare, Tolstoy, Tennyson, and Pasternak), tells us that he set out to write about Lear's poetry. His scope then broadened to a full biography. The resulting publication is a sloppy, rambling story that reads more like a dictaphone transcript than the writing of an Oxford don. Who were the editors, one wonders, who allowed Levi's cliche-laden text ("bright as a button," and "dry as dust") to lurch between impenetrable descriptions ("it is useful to notice at once that Lord Derby's sister Lucy had married the Rev. Geoffrey Hornby of Winwick, because his grandson, who was born in 1799, married the same Mr. Hornby's second daughter, who was his first cousin,") and irrelevant anecdotes ("as for Poole, one of my uncles flew a Turkish flag there, in front of his house by the waterside, but not until the 1880's; in the 1830's his parents were still in Istanbul").

Some simple fact-checking might also have been expected: William Swainson was an *English,* not an American naturalist, John Gould's wife was *Elizabeth,* not Edith, and it was the Goulds, not Edward Lear, who illustrated the zoological findings of Charles Darwin's voyage on the *Beagle.*

The book focuses heavily on Lear's life as an artist, but few of the "wonderful," "charming," "mysterious," or "heavenly" paintings about which Levi raves are illustrated. This leaves the reader with a frustrating sensation of having visited an art museum by telephone and been guided through its disorganized galleries by a docent brimming with strong opinions but few dependable facts. When the artist is allowed to speak for himself, his quotations are not sourced, further reducing the usefulness of the biography.

Lear deserves better, for he is an appealing, important, and intriguingly complex figure whose life at times seems more the stuff of 19th century romance than fact. The 20th of 21 children born to a failed stock-broker and an understandably exhausted mother, Lear was raised by an older sister who gave him his only formal education and his first lessons in art. Lear's bird paintings at the London Zoo and his ambitious, self-financed monograph on parrots so impressed the scientific establishment of his day that the Zoo's chairman, Lord Stanley (later the 13th Earl of Derby) invited him to illustrate the birds and mammals in his private menagerie at Knowsley Hall—a project Lord Stanley had previously discussed with John James Audubon.

Lear enjoyed the financial security and social status such patronage afforded, but he found the detail of scientific illustration extremely taxing. "My eyes are so sadly worse," he wrote John Gould in 1836, "that no bird under (the size of) an ostrich shall I soon be able to see to do." And so with the same intensity he had lavished on birds, Lear turned to landscape, traveling first to Ireland and the English Lake District and then to Rome.

Lear found foreign travel much to his liking and went on to visit Malta, Greece, Turkey,

Albania, Egypt, and Sinai. From these experiences, he produced several color plate books in which he described and illustrated his peregrinations.

One of these books, "Illustrated Excursions in Italy" (1846), brought Lear to the attention of a young Queen Victoria who appointed him as her drawing instructor. Later, Lear returned to Europe and wrote three more travel books. Then, in 1873, he visited India where he felt "nearly mad from sheer beauty and wonder." It was to be the last and most exotic journey of his life.

Peter Levi traces Lear's physical, artistic, and emotional travels with enthusiasm and empathy, but his repeated insertions of unrelated personal anecdote, no matter how well intended, distract from the coherence of the biography. Fortunately, more than a dozen other biographies of Lear have already been written. The best of these, by far, is Vivien Noakes' "Edward Lear, The Life of a Wanderer" (Collins, 1968). While Ms. Noakes' biography (unfortunately out of print) is highly recommended, Mr. Levi's is not.—Robert McCracken Peck

Note.—Robert Peck is currently researching for a book on Edward Lear as a natural history painter. He invites readers with information on this subject to contact him at The Academy of Natural Sciences of Philadelphia, 1900 Benjamin Franklin Parkway, Philadelphia, Pa. 19103; Phone (215) 299-1138; e-mail: peck@say.acnatsci.org.

Polygyny and sexual selection in Red-winged Blackbirds. By William A. Searcy and Ken Yasukawa. Monographs in Behavior and Ecology, Eds. J. R. Krebs and T. Clutton-Brock, Princeton Univ. Press, Princeton, New Jersey. 1995: xviii+312 pp., 61 numbered text figures and 32 tables. $55 (cloth); $29.95 (paper).—The authors note that there have been about a thousand papers published on Red-winged Blackbirds (*Agelaius phoeniceus*). Less than half of these are cited in this monograph because it is limited to the ecology and evolution of polygyny in red-wings and the import of this mating system to the process of sexual selection. The book is no mere synthesis, although the reader is provided with a firm foundation about the behavioral ecology of the species. There is a certain satisfaction in exploring the biology of a species about which a great deal is known, since relevant data are available that are germane to a wide array of questions. Searcy and Yasukawa have used this wealth of published as well as unpublished data to develop arguments related to both proximate and ultimate causes for polygyny and past and present sexual selection. Their analyses of hypotheses are carefully accomplished and fully acknowledge confounding factors, pittfalls, and alternate explanations. Indeed their meticulous, comprehensive approach sometimes caused me to lose sight of where they were going, but fortunately separate discussions within the text of chapters are brought to closure with a summary of their conclusions (or lack of conclusions). This book deserves a longer and more detailed review. I highly recommend that such a review might be the focus of a senior topics course or graduate seminar since there is much to learn, not just about the phenomena discussed, but more broadly, about the support of assumptions and the testing of hypotheses.—John L. Zimmerman.

Bird song: biological themes and variations. By C. K. Catchpole and P. J. B. Slater, illus. by N. Mann. Cambridge Univ. Press, Cambridge. 1995: 248 pp., pen and ink illustrations, 77 figures and 3 tables. $32.95 (cloth).—Bird song arguably is the most intensively studied area of animal communication and has been fertile ground for researchers in behavioral ecology, ethology, psychology, and neuroscience. As such, the breadth and depth of

the literature can prove intimidating to those new to it. Until recently, someone approaching the field faced a vast body of primary literature scattered in a diversity of journals, a handful of specialized review articles, and a few technical edited volumes. Now, however, two of the field's most prominent researchers have written an approachable and comprehensive introduction to the study of bird song.

This book will appeal to graduate students, professionals in the behavioral sciences, and amateur ornithologists alike. The book stands alone, requiring a minimum of background knowledge. However, most of the topics are treated in sufficient depth to serve as a useful academic reference. Catchpole and Slater have not attempted to describe all the available research on a given topic; instead, they select current and representative examples to illustrate their main points. Thus, each section of the book can provide a solid basis for a more intense literature survey of that particular topic.

The production quality of the book is excellent. Crisp pen and ink illustrations introduce each chapter and enhance most figures. The figures are clear and pertinent. The authors also use a standard (author year) citation format—a feature commonly lacking in books aimed at a more general audience. The modest price of this book belies the excellent production job.

In the Tinbergen tradition, the book is organized around questions of mechanism, ontogeny, function, and evolutionary history. Chapter 1 introduces basic nomenclature and concepts in animal communication and bird song in particular. Chapter 2 provides an overview of the physiological and neural mechanisms of song production. This chapter provides a broad, basic introduction to the neuroethology of bird song. Chapter 3 describes the phenomenon of song learning. Again, the chapter is a solid basic introduction to the area. Chapter 4 rounds out the discussion of proximate causation in bird song in reviewing how sound transmission affects singing behavior. This part of the book provides excellent introductions, but many readers will want to follow up the primary literature.

In the remaining chapters of the book, the authors' expertise truly comes to the fore in examining functional causation of song behavior. It is here that bird song is most explicitly considered a product of inter- and intra-sexual selection. Chapter 5 answers the question of which birds sing and when do they do it. Chapter 6 focuses on male-male competition and territory defense in the evolution of singing behavior. Chapter 7 examines mate choice and the role of female song preferences in the evolution of song complexity. Chapter 8 is an examination of the variety of songs and singing behaviors among species and describes competing hypotheses for the evolution of such complexity. Chapter 9 addresses geographic variation in bird songs and the evolution of dialects. This second section of the book provides a balanced view of the debates and controversies that have colored the field. The section also provides an excellent summary of the data we have supporting the functions of bird song: mate attraction and territory defense. On the whole, no other publication on the topic has brought together such a wide body of literature.

In summary, "Bird Song" is the most complete and approachable review of the field to date. Although many experts may find that their particular area has not been covered as thoroughly as they would have liked, or their favorite species has not been used as an example, they will not question the books breadth and utility. I plan to hand a copy to any student interested in starting research in the area. This handsome and affordable volume should complement the bookshelf of anyone interested in bird behaviour.—Scott MacDougall-Shackleton.

NORTH AMERICAN BLUEBIRD SOCIETY RESEARCH GRANTS—1997

The North American Bluebird Society announces the 13th annual grants in aid for ornithological research directed toward cavity-nesting species of North America with emphasis on the genus *Sialia*. Presently three grants of single or multiple awards are awarded and include:

BLUEBIRD RESEARCH GRANT

Available to student, professional or individual researcher for a research project focused on any of the three species of bluebird in the genus *Sialia*.

GENERAL RESEARCH GRANT

Available to student, professional or individual researcher for a research project focused on any North American cavity-nesting species.

STUDENT RESEARCH GRANT

Available to full-time college or university students for a research project focused on any North American cavity-nesting species.

Further guidelines and application materials are available upon request from:

Kevin L. Berner
Research Committee Chairman
College of Agriculture and Technology
State University of New York
Cobleskill, New York 12043

Completed applications must be received by December 1, 1996; funding decisions will be announced by January 15, 1997.

1996 NABS RESEARCH AWARDS

The North American Bluebird Society is pleased to announce the results of its 12th annual research grant's program. The following individuals are recipients of the 1996 research awards:

BLUEBIRD GRANTS

Kristina M. Hannam, University of Miami. Title: Effects of Blowfly Ectoparasites on Eastern Bluebird Reproductive Success.

STUDENT GRANTS

Karl E. Miller, University of Florida. Title: Nest-site Selection and Reproductive Success of Secondary Cavity Nesting Birds in Thinned and Unthinned Slash Pine Forests in Florida.

Paul Doherty, Ohio State University. Title: Metapopulation Dynamics of a Permanent Resident Forest-dwelling Bird Species Within a Fragmented Landscape: Empirical Data and Dynamic Programming Models.

Elena V. Pravosudova, Ohio State University. Title: The Effect of Forest Fragmentation on Social Structure of the Tufted Titmouse.

GENERAL GRANTS

Archibald McCallum, College of Charleston. Title: Reproductive Performance of Flammulated Owls in the Jemez Mountains, New Mexico.

GRADUATE AND POST-GRADUATE RESEARCH GRANTS

The Biological Research Station of the Edmund Niles Huyck Preserve offers grants (max. = $2,500) to support biological research which utilizes the resources of the Preserve. Among the research areas supported are basic and applied ecology, animal behavior, systematics, evolution, and conservation. The 2000 acre Preserve is located on the Helderberg Plateau, 30 miles southwest of Albany. Habitats include northeast hardwood-hemlock forests, conifer plantations, old fields, permanent and intermittent streams, 10 and 100 acre lakes and several waterfalls. Facilities include a wet and dry lab, library, and houses/cabins for researchers. Deadline = February 1, 1997. Application material may be obtained from Dr. Richard L. Wyman, Executive Director, EN Huyck Preserve and Biological Research Station, P.O. Box 189, Rensselaerville, NY 12147.

THE ATLAS OF SOUTHERN AFRICAL BIRDS

Preparation of the manuscript for *The Atlas of Southern African Birds* is nearing completion. The Southern African Bird Atlas Project covers Botswana, Lesotho, Namibia, South Africa, Swaziland and Zimbabwe. Based on seven million distribution records, this is the largest biodiversity project in Africa. The 1600-page, two-volume atlas contains distribution maps and texts for 700 species; for many, the ranges are strikingly different from those shown in current fieldguides and handbooks. 200 vagrants are also covered. To receive publication information, write to the Avian Demography Unit, University of Cape Town, Rondebosch, 7700 South Africa, email adu@maths.uct.ac.za or access the Avian Demography Unit's pages at http://www.uct.ac.za/depts/stats/adu/

ERRATUM

The color frontispiece of *Chlorostilbon olivaresi* in the March 1996 issue of *The Wilson Bulletin* was painted by Eugenia Brieva, staff artist of the Instituto de Ciencias Naturales, Universidad Nacional de Colombia.

INFORMATION FOR AUTHORS

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This issue of *The Wilson Bulletin* was published on 4 October 1996.

The Wilson Bulletin

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The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOL. 108, NO. 4 DECEMBER 1996 PAGES 607–848

(ISSN 0043-5643)

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THE WILSON BULLETIN
(ISSN 0043-5643)

THE WILSON BULLETIN (ISSN 0043-5643) is published quarterly in March, June, September, and December by the Wilson Ornithological Society, 810 East 10th Street, Lawrence, KS 66044-8897. The subscription price, both in the United States and elsewhere, is $40.00 per year. Periodicals postage paid at Lawrence, KS. POSTMASTER: Send address changes to THE WILSON BULLETIN, P.O. Box 1897, Lawrence, KS 66044-8897.

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Printed by Allen Press, Inc., Lawrence, Kansas 66044, U.S.A.

This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).

Frontispiece. The frontispiece painting by Patrick Ching has been made possible by an endowment established by George Miksch Sutton.

THE WILSON BULLETIN
A QUARTERLY MAGAZINE OF ORNITHOLOGY
Published by the Wilson Ornithological Society

VOL. 108, NO. 4 DECEMBER 1996 PAGES 607–848

Wilson Bull., 108(4), 1996, pp. 607–619

DESCRIPTION OF ADULTS, EGGSHELLS, NESTLING, FLEDGLING, AND NEST OF THE POO-ULI

ANDREW ENGILIS, JR.,[1] THANE K. PRATT,[2]
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KIMBERLY M. FLUETSCH[5]

ABSTRACT.—The Poo-uli (*Melamprosops phaeosoma*), a Hawaiian honeycreeper discovered on the island of Maui in 1973 and now near extinction, is represented in museums by only two specimens. Based on the first observations of a nesting pair and re-examination of the two specimens, we describe the adult male and female, eggshells, nestling, and fledgling Poo-uli. Poo-uli are sexually monochromatic but males are brighter. The male is brown above, whitish below, and has an extensive black mask bordered with gray on the crown and a distinct white auricular patch. The female differs in having a similar facial pattern not as sharply demarked and in having a grayish wash below. The observed fledgling resembled the adults but was paler brown above and whitish below and had a much smaller black mask and pale mandible. We tentatively assigned both museum specimens to first basic plumage because they resembled the adult female but retained some pale juvenal coloration in the mandible. We also determined from dissection that the holotype was an immature male; we could not determine sex of the paratype. The nest was an open cup of twigs and bryophytes with a thin lining of fern rootlets. The nest contained eggshell fragments with brown-gray speckling against a whitish background. The nests, eggshells, and nestlings resemble those of other Hawaiian honeycreepers. *Received 1 Dec. 1995, accepted 27 May 1996.*

The Poo-uli (*Melamprosops phaeosoma*), discovered on the island of Maui in 1973, is the most recent, and presumably last, described extant

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genus and species of Hawaiian bird (Casey and Jacobi 1974). Despite doubts about its systematic affinities (Pratt 1992), initial genetic comparisons (C. Tarr and R. Fleischer, pers. comm.) suggest placement of the Poo-uli within the Hawaiian honeycreepers (Fringillidae: Drepanidini). Several studies have investigated aspects of the morphology, life history, and conservation status of this endangered bird (Bock 1978, Baldwin and Casey 1983, Scott et al. 1986, Engilis 1990, Mountainspring et al. 1990, Kepler et al. 1996).

The original description of the Poo-uli was based on two specimens of unknown age, identified as "males (?);" no others have been collected. Subsequent field research has not investigated age and sex differences in plumage and soft parts. No nests had been found until recently. In 1986, Kepler et al. (1996) studied two sequential nesting attempts by a pair of Poo-uli in the Hanawi Natural Area Reserve, Maui. This provided an opportunity to describe the adults, nestlings, fledgling, and nests observed. We compare these descriptions with the two museum specimens, with other Hawaiian honeycreepers and, when appropriate, with cardueline finches, the group from which the Hawaiian honeycreepers are thought to have evolved (James and Olson 1991).

METHODS

Details on the study site and nesting events are given in Kepler et al. (1996), and a map of the study area is provided in Moutainspring et al. (1990) and of the nest site in Engilis (1990). Our descriptions of Poo-uli are based on (1) repeated field observations by Engilis and Kepler with color names quoted from written notes and (2) sketches by Engilis and artist Patrick Ching. We observed birds at the nests from distances of 40 m (nest #1) and 18 m (nest #2) through binoculars (Leitz 10×), spotting telescope (Bushnell Spacemaster 20–60×, nest #1) or Questar telescope (80×, nest #2) (Kepler et al. 1996). Though events at nest #2 were photographed, the pictures taken were only marginally useful for plumage description. Both nests were collected and measured on 16 June 1986, treated by Berlese extraction on 16–18 June, and deposited at Bernice P. Bishop Museum, Hawaii, with the catalog numbers of BPBM 162151 for nest #1 and its eggshell fragments and BPBM 162152 for nest #2. We examined the nests and holotype specimen (BBM-X-147112) at Bishop Museum; M. LeCroy examined the paratype (AMNH 810456) at The American Museum of Natural History (AMNH), New York. We also examined two enlarged black-and-white photographs comparing both specimens soon after preparation and held by the AMNH Bird Dept. Library. The photographs lacked identifying numbers.

RESULTS

Adult Male

Of the two adults tending the nest, we assume that the brighter-colored bird was the male parent because it sang and courted the drab bird, fed the drab bird and chicks, but did not incubate or brood. Also, for all other

Hawaiian honeycreepers, male plumage is either brighter than or similar to female plumage (Freed et al. 1987).

Face.—Face with a distinctive black mask. Mask triangular, crisply bordered, extending from the forehead and chin, around the eye, to a point beyond the eye and bounded above by a gray crown and below by a white auricular patch.

Upperparts.—Crown behind mask gray, merging on the nape to dark brown. Back dark brown. Scapulars and wing coverts dark rufous brown. Primaries and secondaries dark brown with blackish shafts, outer margin of primaries buff. Rump and upper tail coverts rufous-brown. Tail dark brown edged rufous, so short as to be mostly hidden by the folded wings, not tapered, notched, the feathers lax and pointed.

Underparts.—Auricular patch distinct, creamy white continuing onto the throat, bordered by gray of the upper flanks. Chin black. Throat white. Breast white, washed with light gray. Belly white, merging with deep cinnamon undertail coverts. Flanks, forward white washed with gray, posteriorly becoming more grayish tinged buff, then cinnamon. Leg feathering cinnamon. Undersides of the primaries silver-gray.

Bill glossy black, appearing bluish at a distance. Iris medium brown. Legs and feet dark pink-brown; foot pads yellowish.

Adult Female

We assume that the drab bird at the nest was the female, because she incubated and brooded but did not sing. She was similar to but duller than the male, differing as follows. Black mask smaller, more grayish. Pale auricular patch suffused with gray and less sharply bounded. Throat white suffused with gray, but breast and sides to anterior belly gray. Flanks more washed with gray, becoming golden cinnamon where they met the primaries. Leg feathering gray. Undertail coverts buff-gray with darker tips. Bill, iris and legs same as the male. Gape black, anterior roof of palate pink. Neither adult showed signs of pox lesions or scars.

Nestlings

Three nestlings were observed, one in nest #1, two in nest #2. We saw nestlings best on 20–22 May at nest #2 when the oldest chick was ca 10–12 days old. Only their heads could be seen, covered with medium gray natal down; we could not see a black mask. The head of the smaller (younger?) chick, when first seen on 21 May, appeared "mottled" black and gray. For both chicks, the iris was blackish and the bill light gray with bright yellow rim and red spot at the corner of the gape; inside the mouth was reddish pink. On 29 May at ca 19 days-old and 2 days prior

FIG. 1. Detail of Poo-uli chick on 29 May, ca 19 days of age and two days prior to fledging. Note small mask. Tracing from field sketch by A. Engilis, Jr.

to fledging, bill with maxilla slate-gray and mandible underside whitish-cream. Tongue pink.

Fledgling

Of the three chicks observed, one fledged. The fledgling resembled the adults, but its mask was smaller and body plumage paler brown, with less rufous and cinnamon. The small mask was bounded by the dorsal ridge of the bill, distal corner of the eye, and the bill just below the gape, and did not extend onto the chin (Fig. 1). The whitish auricular patch merged ventrally with the darker throat, rather than being sharply outlined. (This description was corroborated on 30 August 1994, when a juvenile Poo-uli being fed by its parents was observed to have a mask "less distinct than the adults, perhaps more gray in color" M. Reynolds and T. Snetsinger, pers. comm.).

Upperparts.—Crown and nape gray-brown, merging with brown back. Back, scapulars, wing coverts medium brown tinged with buff. Rump brown with cinnamon edging, wings and tail dark brown without rufous edging. We did not record obvious wing bars (paler tips of median or greater wing coverts or both), but these could have been indistinct and not noticed or absent altogether.

Underparts.—Inter-ramal space black, chin whitish buff, with some black feathering disconnected to the mask. Throat dingy white. Upper breast gray washed with beige. Belly beige. Vent white. Under-tail coverts cinnamon. Flanks like back, distally becoming cinnamon.

Bill.—Maxilla slate gray, with pale tip. Mandible whitish, with dark edge where the ramphotheca meets the skin. Iris blackish. Gape flange smaller than nestlings', bright yellow, with red spot distally at the corner.

Inside of mouth reddish, with black patch on the roof of the mouth. Legs and feet similar to adults.

Comparison of Observed Birds with Museum Specimens

The holotype and paratype were virtually identical in appearance. Casey and Jacobi (1974) described the paratype as differing from the holotype in (1) its slightly smaller size, (2) somewhat larger mask "slightly mixed and stippled with buff, especially on chin," (3) "upperparts throughout, including crown, duller grayish brown," with less cinnamon, and (4) mandible tipped "only slightly lighter in color, washed with gray rather than shell pink." Photos of the fresh specimens, held by AMNH (one published in Casey and Jacobi 1974), show the paratype's mandible tip as faintly pale and leg color as darker than that of the holotype. LeCroy (pers. comm.) found that the stippling in the mask was caused by pale feathers intermixed with dark ones and that the mandible is now dark throughout.

The adults and fledgling we observed resembled in most respects both the holotype and paratype. In both male and female, the bill was dark throughout in comparison with the pale-tipped mandible of both specimens. The adult male differed most, in its facial pattern of greater contrast and underparts paler, as described above. The adult female differed from the specimens perhaps in having the wings and tail with more cinnamon wash than the paratype (but not the holotype?). The fledgling differed from the specimens in its smaller mask, pale buffy breast, and slate-gray mandible, which in the two specimens was dark with a pale tip. Examination of the two specimens for molt revealed that (1) the holotype either was just completing body molt, with a few new feathers growing on the crown and mask, or was not molting and instead was replacing feathers lost through wear and (2) the paratype showed no evidence of molt and appeared to be in fresh plumage. For the holotype, the distal-most greater wing covert feather on the right wing was buff rather than brown. Flight and tail feathers on both specimens showed little wear.

We add here to the description of the Poo-uli specimens (Casey and Jacobi 1974). We attempted with difficulty to determine the number of flight feathers. There appeared to be nine primaries and nine secondaries for both specimens, and a total of 12 rectrices for the holotype, as in other Hawaiian honeycreepers. We examined flight and tail feathers of both the holotype and paratype for evidence of feather lice, which occasionally are found on other drepanidines, but saw none. Some of the black feathers in the mask of the holotype had brownish centers; the paratype was not examined for this character. The holotype weighed 25.5 g (T. Casey, pers. comm.).

We examined the previously dissected, pickled carcasses of the two specimens. We discovered that the holotype was an immature male by presence of the right testis measuring <1 mm, together with the epididymis leading posteriorly. Sex of the paratype could not be determined by inspection.

Nests

Both nests were open cups and built among the stems of leaf-bearing ohia-lehua (*Metrosideros polymorpha* Gaud.) branchlets (Frontispiece). Distance from the nest base (minus nest tail) to the juncture of the supporting stems measured 60 and 70 mm for nests #1 and #2, respectively. Leafy portions of the stems framed the nests on at least one side and covered the cup of the nests; however, the height and extent of leafy cover was not measured, and cover was cut away from the nests upon collection. For both nests, the branch which joined the supporting stems measured 14.5 mm in diameter below the juncture. Supporting stems incorporated into the frame of the nests were <10 mm diameter and numbered 7 and 6 for nests #1 and #2, respectively.

Dimensions (mm) upon collection for nests #1 and #2 were: (1) outer diameter, 180 by 130 and 180 by 140; (2) outer depth 90 and 110; (3) inner diameter, 70 by 60 and 85 by 60; and (4) inner depth 50 and 40. The body of both nests was constructed of bare twigs of pukiawe (*Styphelia tameameae* [Cham. & Schlechtend.] F. v. Muell.) with coarse mosses filling the spaces between the twigs. Mosses identified from both nests were *Homaliodendron flabellatum* (Sm.) Fleisch., *Thuidium plicatum* Mitt., *Trachypodopsis auriculata* (Mitt.) Fleisch., with nest #1 containing *Aerobryopsis wallicia* (Dozy & Molk.) Fleisch. and nest #2 *Floribundaria floribunda* (Dozy & Molk.) Fleisch. Leaves and stems of graminoids and dicots accounted for <5% of this filling. For the inner 15 mm of nest wall, fern rootlets <1 mm thick replaced pukiawe twigs as the structural frame, with the amount of moss decreasing toward the interior. To the internal surface of this lining was added graminoid fiber, perhaps *Uncinia uncinata* (L. Fil.) Kukenth., 1 mm in thickness. The resulting lining was an open network of fiber. For nest #1, which had been abandoned by the parents three months prior to collection, mosses of the nest body had expanded into the cup, and there were fewer fern rootlets and graminoid fibers. Whether the lack of rootlets and fiber in the first nest is due to differences in original construction, or removal of those materials by the parents or by other birds, is not known. Neither nest contained deposits of fecal matter, supporting the observation that parents removed all feces (Kepler et al. 1996). The nests did not smell of "drepanidine odor" (Pratt 1992) upon collection nor when examined nine years later.

Nest #1 contained eggshell fragments, the largest of which was 9 by 7 mm and, judging from its curvature, may have been from the blunt end of the egg. Though the fragments appeared weathered, they still showed fine, dense, brown-gray speckling against a whitish background.

While the Berlese extraction yielded large numbers of arthropods, no ectoparasitic insects turned up (S. Swift, pers. comm.). Seven diptera larvae and one adult were extracted from nest #1. Most of the mites associated with the nest remain unidentified.

DISCUSSION

Plumage.—Can the age and sex of the two museum specimens now be determined? Given differences in plumage and soft-part colors observed among the sexes and fledgling at the nests, we believe that both the holotype and paratype were hatch-year birds in first basic (post-juvenal) plumage. Dissection confirmed that the holotype was an immature male. Both specimens match most closely the putative adult female, with black mask larger and breast grayer than the fledgling. Both specimens differ from the adults observed at the nest, but resembles the fledgling, in having the mandible not all dark. Both specimens least resemble the putative adult male. We think it very unlikely that either could have been an adult male, especially because adult male drepanidines show little variation within species (Jeffrey et al. 1993, Pratt et al. 1994).

Color of the mandible is important in our determination of the age of the specimens. Unfortunately, the mandible color of the paratype now does not match that in the description and photos of Casey and Jacobi (1974). They described the mandible of the freshly collected paratype as dark with the tip "only slightly lighter in color." The mandible is now dark throughout. The photos show the original description to be correct and that the change occurred post mortem. The slightly darker legs of the paratype in comparison with the holotype evident in Casey and Jacobi (1974: fig. 1) may indicate darkening of the leg color post fledging. However, leg color in life or shortly after death was not noted as different between the two specimens (Casey and Jacobi 1974), and may have either been overlooked, or changed post mortem, or be an artifact of photography. Legs and feet of the observed fledgling were recorded as being similar to those of the adults. This issue can be resolved by future field work.

The specimens fit a presumed plumage sequence for Poo-uli as follows. During the first prebasic molt, juvenal plumage in either sex gives way within a few months of fledging to a female-like first basic plumage, as in many drepanidines. Meanwhile, the mandible color changes from pale to black, with the last vestige of juvenal coloration being the pale tip,

which ultimately darkens. Other drepanidines show a similar change in bill color from light to dark, e.g., Palila (*Loxioides bailleui*; Jeffrey et al. 1993) and Akiapolaau (*Hemignathus munroi*; Pratt et al. 1994). Thus, both specimens show a larger mask than the observed fledgling but apparently still retained the pale-tipped mandible in life. The holotype shows other, less certain signs of first prebasic plumage: a few facial feathers in sheath indicating last stage of molt and a pale brown feather in the greater wing coverts possibly retained from juvenal plumage, as with other drepanidines (Fancy et al. 1993; Jeffrey et al. 1993; Pratt et al. 1994; Lindsey, unpubl. data). For the paratype, the mask shows some pale, perhaps old juvenal, feathers. First prebasic molt is likely to occur in the summer and fall, following breeding, as with other well-studied drepanidines (Jeffrey et al. 1993, Ralph and Fancy 1994). Evidence for seasonality in molt for Poo-uli is lacking. However, the two nests we observed would have or did fledge young in April and June. We add here the above-mentioned observation by M. Reynolds and T. Snetsinger (pers. comm.) of a Poo-uli juvenile on 30 August 1994. The holotype and paratype could have completed prebasic molt prior to being collected in September 1973.

Freed et al. (1987) tentatively characterized sexual chromatism for Poo-uli as monochromatic. We can now modify that to monochromatic with males brighter. In most drepanidines in which the plumage is monochromatic or monochromatic with males brighter, female and first basic plumages approach the bright adult male plumage, whereas juvenal plumages remain distinctly cryptic. Further, in many monochromatic species with males brighter, females show variability, with some females more similar to males than others, e.g., Palila (Jeffrey et al. 1993) and Maui Alauahio (*Paroreomyza montana*; H. and P. Baker, pers. comm.). While Poo-uli are arguably cryptically colored, their most distinctive plumage feature—the black mask with black bill in the center, highlighted behind by the gray crown and white auricular patch—may be a strong intra- and interspecific optical signal (*sensu* Hailman 1977). Viewed head on, Poo-uli provide a striking, unmistakable, and unforgettable image (Fig. 2).

Many drepanidines show a dark loral patch. This patch may have evolved to form an extensive mask in the Poo-uli. Two other, allopatric drepanidines, the Akekee (*Loxops caeruleirostris*) and Hawaii Creeper (*Oreomystis mana*) have independently evolved smaller masks. In all drepanidines with dark lores, including Poo-uli, juveniles show either gray or whitish lores, affirming the importance of dark lores as an adult social signal. Thus, we argue that the mask of the Poo-uli is not a radical departure from the many drepanidine plumage patterns, but instead is noteworthy mainly in degree. If the mask is indeed a strong optical signal, then compared with other monochromatic drepanidines with brighter male

FIG. 2. Poo-uli in first basic or adult female plumage showing bold black mask. Photograph by A. Engilis, Jr.

plumage, Poo-uli also show a convergence of female and first basic plumages with bright male plumage. The difference from other drepanidines is the expression of this character, albeit smaller and grayer, in juvenal plumage as well. Besides the black mask, a likely optical signal and important, ubiquitous field-mark is the cinnamon rump seen as the bird flies away. We encourage other field observers to determine the extent of variation in adult, juvenal, and first basic plumages.

While questioning the systematic position of the Poo-uli, Pratt (1992) claimed "The colors and pattern of the Poo-uli are unlike that of any previously known Hawaiian honeycreeper," and "Thus, plumage color and pattern provide no basis for inclusion of *Melamprosops phaeosoma* among the Drepanidinae." His mis-statement that adult coloration of Poo-uli was gray and white was based on verbal pers. comm. from one of us that we did not have an opportunity to catch in review. Above, we interpret the Poo-uli's black mask as homologous with the black lores or mask of other drepanidines. Brown coloration in immature or adult plumages is shared by five other historical Hawaiian honeycreepers (Akepa, *Loxops coccineus*; Apapane, *Himatione sanguinea*; Greater Koa-Finch, *Rhoda-*

canthis palmeri; Kakawahie, *Paroreomyza flammea*; Ula-ai-hawane, *Ciridops anna*).

Why are Poo-uli brown, an unusual color for a Hawaiian honeycreeper? Mountainspring et al. (1990) document substrate-restricted foraging by Poo-uli on branches where they glean or forcibly excavate invertebrates from bark, lichens, and moss mats. Mountainspring et al. (1990) speculated that Poo-uli also foraged on the ground, partly suggested "by the bird's drab color and stout pedal morphology." They went on to compare Poo-uli coloration with that of ground-foraging antbirds. Poo-uli have seldom been seen at ground level (Mountainspring et al. 1990), but this could result from the difficulty of potentially observing such behavior in the dense understory that prevails in its range. Nevertheless, comparison with other branch-foraging specialists is also appropriate. Passerines specialized for taking insects from bark or epiphytes include members of the Furnariidae and Troglodytidae in Costa Rica (Sillett 1994), Certhiidae in North American alder rainforests (Stiles 1978), and Paradisaeini (Corvidae) in New Guinea (Pratt and Stiles 1985). All share brown plumage (except adult male and some female birds of paradise) and stout pedal morphology. Thus, brown plumage of Poo-uli may have evolved independently as cryptic coloration associated with foraging for invertebrates on branches.

Eggshells and nestlings.—In background color and spotting color and pattern, the Poo-uli eggshells resembled eggs of other drepanidines, e.g., Common Amakihi (*Hemignathus virens*) and Palila. The Poo-uli eggshells, together with eggs of most drepanidines, differ in color from eggs of most cardueline finches in having the background whitish rather than tinged with blue or green (Newton 1972). The Poo-uli nestlings share gray down on the head and a pinkish-red gape with nestlings of nine other drepanidines: Akikiki (*Oreomystis bairdi*), Anianiau (*Hemignathus parvus*), Apapane, Crested Honeycreeper (*Palmeria dolei*), Common Amakihi, Kauai Amakihi (*Hemignathus stejnegeri*), Iiwi (*Vestiaria coccinea*), Maui Alauahio, and Palila (Eddinger 1970; Berger 1981; van Riper 1987; H. and P. Baker, F. Duvall, Jr., pers. comm.; T. Pratt, pers. obs.). The yellow gape flange of Poo-uli chicks matched the flanges of these species, which vary from yellow to cream. However, the red spot in the corner of the gape flange and the dark area observed on the Poo-uli nestling's palate (which may have been due to shading and therefore possibly irrelevant) have not been mentioned for the other species.

Nests.—The Poo-uli nests we collected are similar to open cup nests of other drepanidine and cardueline species. In gross stucture and placement, the two Poo-uli nests resembled nests we have collected and examined of such widely divergent Hawaiian honeycreepers as Apapane,

Common Amakihi, Crested Honeycreeper, Iiwi, Maui Alauahio, and Maui Parrotbill (*Pseudonestor xanthophrys*) in the same habitat on Maui and for the honeycreeper nests studied on Kauai by Eddinger (1970). The Poo-uli nests differed from those of other honeycreepers primarily in the species of plant materials and in size. However, the materials were of plant species common near the nest site, and the nests seemed to fit well within the size gradient of drepanidine nests relative to bird body size. In their loose structure and moss matrix, the Poo-uli nests most closely resembled nests of the slightly larger Crested Honeycreeper. The Poo-uli nests differed most from the smaller Maui Alauahio nests in being less finely and compactly woven and in building materials. Consistent composition between the two Poo-uli nests and their unique component plant materials may be the result of their being built in the same locality by the same pair of birds. A larger sample of nests would probably reveal variability in Poo-uli nest construction and placement. The Poo-uli nests resemble the description of the "commonest type" of nest for cardueline finches in Europe (Newton 1972:175). This type was described as "rather bulky and made of various flexible materials, often with a base of twigs and bents, a main structure of grass and moss, and a lining of hairs and rootlets." The Poo-uli nests differ from this description in their near absence of graminoid leaves and hair, materials rare in the bird's habitat.

Implications for conservation.—We draw attention to the following new aspects of Poo-uli natural history that bear on its conservation. Information on age and sex differences in plumage characters will help investigation of the species' demography. However, because our conclusions are based on very few individuals, other field workers should attempt to further explore variability in characters used for ageing and sexing Poo-uli.

We note the low wing/tarsus ratio of 2.74 and 2.88 and short tail of 38.0 and 36.5 mm, for the holotype and paratype, respectively (measurements from Casey and Jacobi 1974). This ratio and tail length are the smallest for the ten historic honeycreeper species from Maui (from measurements in Amadon 1950). The low wing/tarsus ratio, the short rounded wings, and extremely short tail of the Poo-uli may be clues to its mobility. Poo-uli are capable of short flights only and may be confined to home ranges smaller than those of most Hawaiian honeycreepers.

ACKNOWLEDGMENTS

We thank the Hawaii Dept. of Land and Natural Resources and U.S. Fish and Wildlife Service for supporting our study and for aggressively pursuing restoration of the Poo-uli; Tom Hauptman for many memorable chopper flights; Allen Allison, Patrick Ching, Betsy Harrison-Gagne, Larry Katahira, Jim Krakowsky, Joan Suther, and Rick Vetter for assistance

in observing Poo-uli at their nests; Phil Bruner and Allen Allison for collecting inactive Poo-uli nests; Michelle Reynolds and Tom Snetsinger for sharing their observations of Poo-uli; Mary LeCroy for examining the paratype; Warren Wagner and William Hoe assisted by Clyde Imada for identifying angiosperm and bryophyte components, respectively, of nests; Sabina Swift and Gordon Nishida for identifying arthropods extracted from nests; Helen and Paul Baker for showing T. Pratt their large collection of Maui Alauahio nests; Cheryl Tarr and Rob Fleischer for sharing preliminary findings on molecular evolution in Poo-uli; Allen Allison, Carla Kishinami, and staff at Bishop Museum for facilitating research at their collection; Patrick Ching for permission to reproduce his painting; Paul and Helen Baker, Tonnie Casey, Fern Duvall, Jr., Steve Fancy, Jim Jacobi, and Mary LeCroy for reviewing drafts of this article.

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COLOR PLATE

Publication of the frontispiece painting has been made possible by an endowment established by George Miksch Sutton.

Wilson Bull., 108(4), 1996, pp. 620–638

NESTING BEHAVIOR OF THE POO-ULI

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Abstract.—We describe two sequential nestings of a pair of Poo-uli (*Melamprosops phaeosoma*), a Hawaiian honeycreeper nearing extinction. Similarities to nesting of most other honeycreepers included: nest site in ohia lehua (*Metrosideros polymorpha* Gaud.) canopy; breeding in March through June; monogamous breeding system with the putative male helping build the nest, feeding the putative female throughout each nesting event, and feeding the chicks, but not incubating or brooding; and complete nest sanitation. Notable differences were the paucity of songs and calls by the parents and inclusion of snails in the diet of nestlings. Clutch size was probably two eggs for both nests. High winds, rain, or both influenced parental behavior: the female stayed longer on the nest and took shorter recesses in poor weather. Weather did not affect rates at which the male fed the female on the nest; however, the feeding rate increased from the egg to the chick stage probably because food was passed on to the chicks. At nest #2, parents fed young chicks (<14 days old) more often in good than in poor weather; data were insufficient for old chicks. Weather is usually poor throughout the year in the relictual range of the Poo-uli and is likely to impact nesting success. The first nest failed in poor weather. The second fledged a single young 21 days old. Diet of nestlings appeared to consist of a higher proportion of insect larvae than that of older birds, which are reported to eat mostly snails. *Received 12 Dec. 1994, accepted 27 May, 1996.*

Few endangered birds are closer to extinction than the Poo-uli (*Melamprosops phaeosoma*), a monotypic species and genus of Hawaiian honeycreeper (Fringillidae; Drepanidini). Since its discovery on Haleakala Volcano, Maui Island in 1973 (Casey and Jacobi 1974), the Poo-uli population has fallen from several hundred to fewer than 10 birds today, and it is extinct at the type locality (Scott et al. 1986; Engilis 1990; Mountainspring et al. 1990; J. Simon and M. Reynolds, pers. comm.).

Why is the Poo-uli disappearing? Past research has been sporadic and underfunded; consequently the life history and population ecology of the bird are poorly understood. Field work has also been hampered by logistical difficulties, inhospitable conditions, and the bird's low population density and lack of vocal activity. Nevertheless, scant data (Casey and Jacobi 1974, Baldwin and Casey 1983, Engilis 1990, Mountainspring et

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al. 1990) and conjecture based upon biology of other honeycreepers (Kepler et al. 1984; Scott et al. 1986; van Riper et al. 1986; Engilis 1990; Mountainspring et al. 1990; Atkinson et al. 1995) implicate habitat damage by feral pigs (*Sus scrofa*), predation by and competition with non-native small mammals, increased risk to avian disease below 1800 m elevation, and the untested hypothesis that the bird's molluscan prey base is also dwindling. The poo-uli's substrate-restricted foraging for arthropods and molluscs in bark and epiphytes (Mountainspring et al. 1990) implies ecological specialization vulnerable to environmental change brought about by the invasion of non-native organisms. So far, recovery efforts begun in 1990 have focused not on the poo-uli, but on successful habitat restoration through pig removal and exclusion. Recently, the National Biological Service, funded and otherwise supported by other agencies (see Acknowledgments), initiated a program for research and restoration of the Poo-uli.

In 1985–1986, Kepler and Engilis studied aspects of the ecology of endangered Maui birds, including the Poo-uli (Mountainspring et al. 1990) at Hanawi Natural Area Reserve. In 1986, they discovered and monitored two active nests of a pair of Poo-uli. Our purpose is to describe events at these nests in as much detail as possible, because (1) this is the only information on Poo-uli reproduction, (2) recovery efforts, in the field and in captivity, will benefit from knowledge of the natural history of the species, and (3) the Poo-uli may go extinct, leaving no further record. We compare behavior of the Poo-uli with that of other Hawaiian honeycreepers and mainland cardueline finches, from which the honeycreepers are descended (James and Olson 1991). We also discuss how this information may help the species' survival.

STUDY SITE AND METHODS

The two nests were within about 30 m of each other along a small, eastern tributary ravine of the east fork of Hanawi Stream at 1800 m elevation. Nest #1 was situated on a small ridge crest, more exposed to prevailing trade winds than nest #2, which was on the east flank of the same ridge about 15 m above the ravine floor. Both were within 100 m of a headwall of the Hanawi gulch. Vegetation at the site was Mixed Shrub Montane Wet Forest (Jacobi 1989) with mean canopy height of 13 m and crown cover averaging 60% and dominated by ohia lehua (*Metrosideros polymorpha* Gaud.) (Mountainspring et al. 1990). Damage to vegetation by feral pigs appeared slight, with the under story largely intact. Rainfall, brought year-round predominantly by NE trade winds, was estimated to exceed 3 m per annum.

Nest #1 was built in a canopy ohia lehua 15 m tall. Vegetation surrounding the nest tree included (1) a subcanopy kolea tree (*Myrsine* sp.) and pukiawe shrub (*Styphelia tameiameiae* [Cham. & Schlechtend.] F. v. Muell.) where the male often fed the female, and (2) a dense understory of shrubs and ferns used as cover by the birds when approaching or leaving the nest area. The nest was located in a secondary, horizontal branch in the lower crown, 8 m

TABLE 1
DATES OF OBSERVATION AND NEST STAGES

	Dates	Stage
Nest #1	5–6 March	Nest construction, courtship
	17–20 March	Eggs
	24–26 March	Eggs hatch 25 March; nestling
	31 March to 3 April	Nestling; first seen April 2
	7 April	Nestling
		Nest fails 8–14 April
Nest #2	16 April	Nest construction
	9–14 May	Eggs hatch 11, 13 May; nestlings
	19–22 May	Nestlings
	29–31 May	Nestlings, one fledges on 31 May
	1 June	Fledgling

above ground, and was incorporated into live twigs and small branchlets a few cm below live foliage. The nest site was exposed to some direct sunlight in the morning and was sheltered from trade winds, but it swayed in an arc of ca 1 m in SE winds >13 $km \cdot h^{-1}$. The globular, open cup nest was composed of sticks, mosses, and plant fiber (Engilis et al. 1996). Two other, inactive and unidentified nests occupied foliage above and below on the same branch. During nest construction, the male infrequently visited a fourth, triangular nest 4 m up in a 5-m ohia lehua sapling within 10 m of the nest tree. Based on the construction and location of this nest, we believe it was built by a non-native Red-billed Leiothrix (*Leiothrix lutea*).

Nest #2 was also built in an ohia lehua tree surrounded by similar vegetation. Nearby pukiawe and kanawao (*Broussaisia arguta* Gaud.) shrubs provided nest material. This nest was placed in the tree in a position very similar to nest #1. The nest was only 8 m above ground and sheltered from NE trades, being situated in the SE (140°), uphill portion of the crown, and 5–10 m lower than the crowns of nearby ohia lehua. It was, however, exposed to SE winds which caused the nest branch to sway 1–2 m. No other nests were noted in the tree.

Only two Poo-uli were observed tending the nests. These care-givers, likely the same two birds at both nests, were recognized by plumage characters (Engilis et al. 1996). We assume the brightly colored bird was the male and the drab bird was the female. Viewed closely, neither showed lesions of active or past infection from avian pox that might have influenced their behavior.

We studied both Poo-uli nests for periods of one to five days, from nest construction until fledging or failure (Table 1). We observed Poo-uli at the nests from a distance of 40 m (nest #1) and 15 m (nest #2) through binoculars, spotting telescope (Bausch & Lomb 30×, nest #1) or Questar telescope (80×, nest #2) from under a tarp shelter. A creek separated observers from both nest trees, and when flowing vigorously it prevented us from hearing Poo-uli vocalizations, especially at the more distant nest #1. On most days, weather permitting, observers watched the nest continuously from 08:30 to 17:00 (all times are Hawaii Aleutian Times). We did not approach the nest trees while nests were active. Our presence did not appear to influence the birds' behavior at nest #1, but may have done so at the closer nest #2 (see below). From the observation points, we could usually view parental

behavior at the nests, but we could not see the nest contents until the nestlings were old enough to reach above the nest rim. We recorded: duration of behaviors at the nest to the nearest 10 sec, vocalizations, and feedings and other behaviors off the nest. We mapped the birds' movements to and from the nest.

At times, heavy rain or fog prevented accurate observation; these data were omitted from analyses. We estimated heights and distances to the nearest meter. We recorded percent cloud cover, rain scores (0 = none; 1 = mist; 2 = drizzle; 3 = light rain; 4 = downpour), and wind scores by the Beaufort scale. Once inactive, both nests were collected and deposited at the B. P. Bishop Museum, Honolulu (Engilis et al. 1996).

The Questar enabled us to identify some prey items brought to nest #2. We identified prey items as (1) caterpillars, for larvae colored other than white or pink; (2) pale larvae, for larvae colored white or pinkish, which likely were bark-dwelling coleoptera or lepidoptera; (3) beetles; (4) succineid snails (Succineidae); and (5) snails, for unidentified snails. Mountainspring et al. (1990) described foraging observations in vicinity of the nests.

We assigned observations to the incubation stage at nest #1 prior to 12:00 on 25 March and at nest #2 prior to 10:00 on 11 May; observations afterwards were assigned to the nestling stage. We categorized nestlings as young (<14 days) or old, based on the assumption that they were partly feathered, thermoregulating, and required less brooding by the parents at about 14 days age or older.

Time on the nest is the length of the visit to the nest; time off is the time from when the bird left the nest until it returned. Preliminary models using stepwise linear regression indicated that both wind and rain significantly affected time spent by the female on and off the nest. We created a combined weather variable that was coded as "poor" whenever winds exceeded 8 $km \cdot h^{-1}$ (Beaufort scale 2) or rain occurred (rain score >1) or both; otherwise, we coded weather as "good." The models also showed that nest number significantly affected time spent by the female on and off the nest, being longer for both at nest #2. Nearness of observers to nest #2 may have caused the female to hesitate leaving or returning to the nest. Consequently we analyzed nests separately for time spent by the female on and off the nest.

We compared rates of the male feeding the female at both nests combined and of parents feeding chicks at nest #2 (better visibility) using a test of comparison for two Poisson processes (Cox and Lewis 1978:225). Sample units were daily rates calculated separately for good and poor weather. Values of $P < 0.05$ were considered statistically significant.

RESULTS

Behavior

Nestbuilding.—Nest #1 was under final construction by one or both Poo-uli when discovered and first observed at 13:15–16:37 and 07:24–14:00 on 5 and 6 March, respectively. At that time, we did not record observations systematically. In the vicinity of the nest tree, the birds moved through the subcanopy of the forest at 5–12 m. They were exceptionally active for Poo-uli, moving quickly in the subcanopy, pausing at times to preen, forage or gather nest material such as moss from ohia lehua branches. When arriving in the nest tree, the birds flew quickly to the nest; when leaving, they often dropped vertically from the nest, dashing away above the undergrowth, then ascending trees distant from the nest. Both birds visited the nest with about equal frequency; however, we

did not determine if one or both performed nest construction. The male was observed singing repeatedly at and near the nest and while courting the female. Dense fog frustrated further observation on the second day. Once incubation began, we did not observe either parent taking building materials to the nest and assume that nest construction had ceased.

Nest #2 was also under final construction when discovered on 16 April. At nest site #1 at 12:10–16:00 on 14 April, we detected the male and female foraging and giving whistles and chit-chit calls 18 times, but did not hear song or observe nest-building. The pair was associated tightly, and we observed courtship feeding. We again visited the site at 10:55–14:50 on 16 April and observed the Poo-uli carrying material to a new nest at 12:00–13:24. Though both parents were present, the female was only once seen carrying material to the nest (moss collected near the ground), while the male was seen carrying material to the nest nine times (six times with twigs and three with moss). Twigs were collected three times from a pukiawe shrub, and moss was gathered three times, <1 m from the ground, in a kanawao shrub. We did not see either bird actually build the nest. The pair was silent during construction of this nest. Once incubation began, we observed the female add new material to either nest only once.

Courtship.—We observed courtship during nest-building only at nest #1, at 13:45–13:50 on 6 March. The male was detected singing and displaying to the female 12 m up in a 15 m ohia lehua tree distant from the nest. While the female stood still, the male circled her, wing-flicked, and delivered six songs in about 30 sec. The female then flew into the nest tree, with the male following and singing in flight. The female moved close to the nest; the male joined her and continued circling and singing eight songs in about 30 sec. The female then returned to her previous location in the distant tree, the male following and singing. Singing and chasing continued, screened from view.

Egg stage.—We observed nest #1 for 24.3 h in six days and nest #2 for 11.5 h in three days during the egg stage. At nest #1, egg(s) were laid either during 8–17 March (by 18 March the female incubated continuously) or on about 10 March, assuming an incubation period of 16 days and hatch date of 25 March. At nest #2, eggs were laid on about 26 and 27 April, assuming hatch dates of 11 and 13 May (see below). Laying of the second clutch followed 13–19 days after failure of the preceding brood. Clutch size was not determined but is assumed to be two, because at nest #1 we saw only one nestling and watched the female eating an egg, nest #2 contained two chicks, and when collected the nests contained neither remains of other eggs nor chicks.

Only the female incubated at both nests. Behaviors of the incubating female included inactivity, shifting position in the nest, breast pumping motions as she settled on eggs, preening, adjusting nest material, accepting food from the male, and manipulating objects inside the nest (probably turning the egg). She was also observed resting with eyes closed for a few seconds on nest #2 during the day. The incubating female crouched low in the nest with her head tilted upward so that her eyes peered just over the rim of the nest; at times she crouched so low that she was not visible. Occasionally, she would turn and face a different direction. Both she and her mate approached and left the nest tree quickly and deliberately from several favorite routes. They usually arrived at the nest by flying first into the nest tree, then hopping towards the nest. They usually departed from the nest directly, not via the nest tree.

The female recessed to defecate, to be fed by the male, to forage, and to perform other activities. Both sexes often wing-flicked in vicinity of the nest, and the female bill-wiped on branches while approaching the nest. The female sometimes recessed only to defecate copious white feces, which she did in the nest tree or from nearby vegetation; she then returned immediately to the nest. The male usually consorted with the female when she recessed and was observed feeding her during recesses, either in the nest tree or in nearby vegetation.

The female was fed by the male both on or off the nest. She solicited feeding by wing-fluttering or -quivering, and rarely by vocalizations audible to observers. At nest #2, we observed these feedings in better detail during the chick stage: when on the nest and anticipating the male's approach, she would point her bill up and begin bill-clapping with increasing frequency as the male neared. She was rarely heard giving a faint two-note call prior to the male's arrival, but this vocalization was hard to hear and could have gone unnoticed most of the time. All observations of food transferal were of regurgitation rather than of carrying and transferring food in the bill. The male delivered boli of food into the female's gaping mouth in the same way that he later fed the chicks. During feedings, the male perched on the same level or above or below her. The female often left the nest shortly before or as the male approached; by what cues she detected his approach are not known, perhaps by sight or by faint chit-chit calls rarely heard by us. We believe that the male fed the female during most recesses, because recesses were usually too short for the female to forage profitably and because on many brief recesses the male and female were seen consorting in dense cover, where they could not be further observed.

During the egg stage, the male was usually seen visiting the vicinity of the nest before or during the female's recesses or when he fed the

female on the nest. Twice, he chased the female in the nest tree. During a heavy rain he loafed, preened, and head-scratched under the shelter of a branch in the nest tree. Though he sometimes foraged in the vicinity of the nest tree, his usual long absences followed by his arrival and immediate feeding of the female suggest that he foraged mostly beyond view of the nest.

Nestling stage—parental behavior.—We observed nest #1 for 46.2 h during seven days and nest #2 for 66 h during 11 days of the nestling stage. We believe we observed hatching at both nests. At nest #1, we first saw a chick on 1 April. However, we suspect hatching occurred much earlier, perhaps on 25 March, when at 11:44, the female, incubating but fidgeting, hopped onto the nest rim and extracted from the nest cup a "flesh-colored object" 4 cm long and "flaccid," which she immediately consumed. The observer questioned whether she had eaten one of her own eggs. We doubt that the object was a hatched eggshell, because it didn't look like one, and other honeycreepers discard shells away from the nest (T. Pratt, pers. obs.). We also doubt it was a food item, because the female's last feeding was 17 min earlier, or a fecal sac of a small chick. Also, from that day onward, we noted that the female more frequently directed her attention to the interior of the nest. We assume that the observer had witnessed the female eating the contents of a broken egg or a dead chick.

At nest #2, the first hatching probably occurred on 11 May. The day previous, the female incubated uneventfully. On the morning of 11 May, she frequently interrupted incubation and directed her attention to the nest interior, and for the first time the male was seen checking the contents of the nest. Based on the parents' behavior, we believe that hatching occurred at about 10:00. At 11:02, the female may have fed a chick, and by the end of the day one definite feeding was observed. The second chick may have hatched on 13 May. On four occasions from 09:45 to 11:40 on 13 May, the female flicked objects that looked like eggshells (or fecal sacs?) from the nest. Afterwards, the male and female were observed simultaneously feeding chicks at two locations in the nest. We first observed a chick on 19 May. We could not determine the initial brood size at either nest, but observed only one chick at nest #1 and two chicks at nest #2, once the chicks began to lift their head above the nest rim.

Only the female brooded. Behaviors of the female at the nest were similar between the egg and nestling stages, but now included a behavior we call "nest-treading," feeding and grooming the chicks, nest sanitation and maintenance, drinking water drops from twigs, and an occasional brief nap. Nest-treading involved the brooding female treading the floor and inside walls, perhaps either to adjust her position and the chick's or

to stretch and enlarge the nest cup. The female fed the chicks with food she had collected herself, but more often with food given to her by the male at or away from the nest. Both parents carried food internally, rather than in their beak. However, during the old chick stage, food was sometimes carried in the beak. Fecal sacs were eaten, flicked over the side of the nest, carried and discarded away from the nest, or transferred from the female at the nest to the male to take away. Nest sanitation must have been efficient, because feces were not observed on the rim of the nests or found when the nests were collected. Behaviors of the female on recess did not change between the egg and nestling stages, except that in addition she discarded fecal sacs.

The male continued the same patterns of activity as during the egg stage. Though he fed the female on nest #1, he was not observed feeding or tending the nestling. Absence of observed care-giving by the male towards the chick at nest #1 may have been due to difficulty in viewing that nest, rather than an absence of such behavior. At nest #2, beginning on hatching day, the male frequently fed the female and nestlings and removed fecal sacs. On the day prior to fledging, the male on a few occasions delivered food to the nest by carrying a succineid snail in his mouth rather than internally.

Nestling stage—chick development.—Chicks remained huddled under their mother throughout the first two weeks in the nest and were usually seen only when they lifted their heads to feed. At nests #1 and #2, chicks were first seen, begging, on 2 April and 19 and 21 May (observers absent 15–18 May), respectively, when each attained nine days of age. Our data on the behavior of older nestlings is sketchy because chicks were observed for only three days during their last week in the nest. Nest #1 failed in a downpour of 350 mm rain during 8–14 April. Nest #2 fledged one chick on 31 May; fledging may have been delayed by weather, which was poor the day before fledging. The smaller and by then much weaker chick was last seen gaping on 29 May and is presumed to have died in the nest, though its remains were never found. In the two days prior to fledging, the surviving chick, when unattended, spent most of its time resting, preening, exercising in short bouts of wing-flapping, and drinking water off plant material. When fed, it flapped its wings vigorously. We never heard it call. Besides relying on its parents for nest sanitation, the chick also defecated over the side of the nest.

On 31 May, the day it fledged, the chick made several excursions to branches in the immediate vicinity of the nest, at first returning to the nest to be fed, then leaving the nest for feeding. It was first heard giving single, infrequent chip notes. Though the female brooded the chick on five occasions, the chick sometimes resisted by pushing her off the nest.

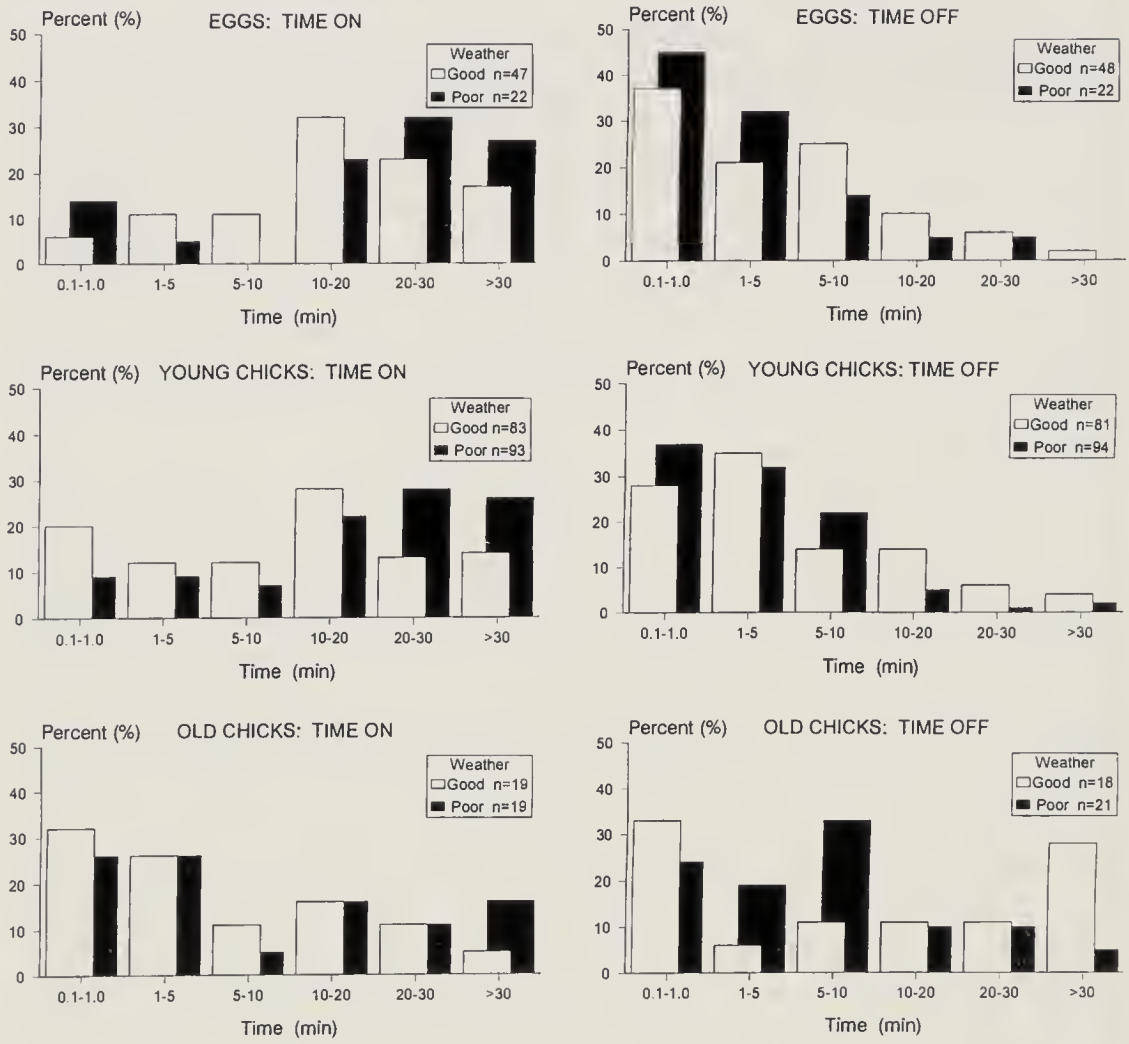

FIG. 1. Frequency distribution (percent observations) of incubation, brood, and recess times of the female Poo-uli in good vs poor weather at nests #1 and #2 combined. Poor weather had winds >8 km·h^{-1} or rain or both. Shown are times for three stages: eggs, young chicks (<14 days old) and old nestlings (≥14 days).

Shortly after 16:30, the chick fledged and moved into the canopy of the nest tree. It was 21 days old.

Fledgling stage.—We observed the parents attending the fledgling during 09:00–12:54 on 1 June. The fledgling was located in a 7 m tall pukiawe tree near the nest tree. It seemed to be alone, loafed most of the time, and remained in the subcanopy. It was capable of short horizontal flights. Both parents provided food. Though the parents occasionally gave chit-chit calls, the chick could not be heard. It wing-quivered while begging and moved about awkwardly.

Rates of incubation, brooding, and feeding.—Weather affected time spent on and off the nest by the female during the egg and young chick (<14 days old) stages (Fig. 1, Table 2). The female at nest #1 spent more

TABLE 2

TIME (MIN) SPENT BY THE FEMALE POO-ULI ON AND OFF THE NESTS IN GOOD VS POOR (WINDS > 8 KM-H^{-1} OR RAIN OR BOTH) WEATHER DURING STAGES OF EGGS, YOUNG CHICKS (<14 DAYS OLD), AND OLD CHICKS (≥14 DAYS OLD)

		Nest #1					Nest #2				
		Time on			Time off		Time on			Time off	
Stage	Weather	N	Mean	SE	Mean	SE	N	Mean	SE	Mean	SE
Egg	Good	41	14.5	2.25	6.3	1.25	18	25.0	2.12	7.7	3.05
	Poor	18	25.1	7.43	4.2	2.25	11	24.9	4.38	3.9	1.24
Young chick	Good	51	15.2	1.63	2.7	0.46	47	12.4	2.19	11.5	1.79
	Poor	62	21.0	2.17	1.7	0.30	53	25.9	3.02	8.2	1.43
Old chick	Good						19	7.9	2.41	18.2	5.18
	Poor						25	11.2	3.04	8.6	2.09

time on the nest during poor weather (mean ± SD = 21.8 ± 17.6 min) than during good weather (14.9 ± 11.5 min; two-way ANOVA, $F_{2,132} = 3.91$, $P = 0.02$). Nest stage (eggs vs young chicks) did not significantly affect time spent on the nest for nest #1 ($F_{1,132} = 0.34$, $P = 0.56$), but the length of recesses was longer when the female was incubating (5.7 ± 7.3; $F_{1,137} = 12.02$, $P = 0.0007$) than when she was brooding young chicks (2.2 ± 2.7 min). Length of recesses at nest #1 was 4.2 ± 5.33 min during good weather and 2.2 ± 4.11 min during poor weather, but was highly variable ($F_{2,137} = 2.34$, $P = 0.10$).

For nest #2, nest stage and weather affected both time on the nest (two-way ANOVA, $F_{6,137} = 5.86$, $P = 0.0001$) and time off the nest ($F_{6,135} = 2.11$, $P = 0.056$). Time spent on the nest (mean ± SD) was 25.0 ± 10.1 min for egg, 19.5 ± 18.4 min for young chick, and 9.5 ± 11.9 min for old chick (≥14 days old) stages. Pairwise comparisons of means showed that differences were not significant between egg and young chick stages, but significant for young chick and old chick stages (Tukey's test, $P < 0.05$). Mean time spent on the nest was 14.1 ± 13.1 min during good weather and 21.8 ± 18.5 min during poor weather. Mean length of recesses was 6.4 ± 10.5 min for egg, 9.7 ± 10.0 min for young chick, and 13.0 ± 17.0 min for old chick stages. None of the pairwise comparisons of means was significant (Tukey's test, $P < 0.05$). Recess time was 12.4 ± 15.3 min during good weather and 7.8 ± 8.8 min during poor weather, again highly variable.

The daily rate at which the male fed the female while she was on the nest was not statistically different between good and poor weather during both the egg stage (0.23 vs 0.66 feedings·h^{-1}; 22.0 and 12.1 h, respec-

TABLE 3
NUMBERS OF IDENTIFIED FOOD ITEMS TRANSFERRED FROM MALE TO FEMALE OR FROM ADULTS TO CHICKS AT NEST #2

Chick age[a]	Number of feedings	Caterpillars	Pale larvae	Succineid snails	Other snails	Beetles	Total
1–4	8	6+	3	0	(8?)	0	9 or 17
10–12	12	17	9	(2?)	0	0	26 or 28
19–21	32	30	17	34	4	1	86

[a] Age of the oldest chick in days.

tively; $Z = 1.687$, $P = 0.091$) and the young chick stage (1.08 vs 0.95 feedings·h^{-1}; 30.5 and 49.5 h, respectively; $Z = 0.556$, $P = 0.582$). Rates of the male feeding the female increased significantly from the egg to young chick stage (0.38 vs 1.00 feedings·h^{-1} incubation or brooding; 34.1 and 79.9 h, respectively; $Z = 4.03$, $P = 0.0001$), because the male's main purpose for visiting the nest was to feed the chicks directly or via the female. During the old chick stage, the female spent little time on the nest, and consequently there were few male-to-female feedings.

Feeding rates of chicks varied with sex of parent and weather at nest #2. The female fed young chicks at a significantly greater rate than did the male (1.77 vs 1.03 feedings·h^{-1}, 43.6 h observation; $Z = 2.920$, $P = 0.004$); however, the increased male-to-female feedings were likely passed on to the chicks by the female, so that the male's role in providing food to young chicks could have been the same or greater than the female's. For older chicks, feeding rates by female vs male showed no significant difference, perhaps due to small sample size (1.60 vs 2.24 feedings·h^{-1} in 15.6 h; $Z = 1.290$, $P = 0.197$). Parents fed young chicks more often in good than in poor weather (1.95 vs 1.04 feedings·h^{-1} in 17.2 and 26.5 h; $Z = 3.257$, $P = 0.001$); data were insufficient for old chicks.

Diet.—We cannot state whether items identified represent the complete diet, because we could not view or identify most food transferred, and in cases when we did recognize food items, these were only one or a few items in each transfer. Most food appeared as indeterminate goop. Most food items identified were lepidoptera and coleoptera larvae (Table 3). Molluscs did not appear for certain in the food until the chick was near fledging, when succineids became an important dietary component.

Interspecific interactions.—The Poo-uli did not actively defend their nests from approaches by other honeycreepers. We recorded 14 approaches to within 2 m of nest #1: 11 by Apapane (*Himatione sanguinea*), 1 by either an Apapane or Iiwi (*Vestiaria coccinea*), 1 by a Common Amakihi (*Hemignathus virens*), and 1 by a Maui Alauahio (*Paroreomyza mon-*

tana). In nine approaches, the female was incubating or brooding and did not respond, apart from watching the intruder or crouching lower in the nest. In two of five instances when the female was off the nest and an intruder approached, the male or female drove the intruder (Apapane) away with displays and chasing. When displaying, the Poo-uli crouched and, with neck extended forward, faced the intruder. In both instances, we believe the nest was at the egg stage. On 14 April, after nest #1 was abandoned, Apapane entered it several times, presumably collecting nesting material. Apapane gather building material from nests of other birds (Eddinger 1970).

Vocalizations

When not breeding, Poo-uli vocalize infrequently (Engilis 1990, Mountainspring et al. 1990). Their calls are inconspicuous and very simple in structure, consisting mainly of chit (chip, whit, or tch) notes given singly, in couplets, or in short bursts (see Pratt 1992 for sonogram). Vocalizations given while nesting are similarly rare and quiet.

Song.—A single male song on 5 March initially alerted us to a possible nest; yet, only one song was heard from 13:15 to 16:35. Songs were heard more frequently on 6 March when nest #1 was still under construction, twice on 17 March early in the egg stage, and not at all later. The male's song consisted mainly of paired couplets in iambic pattern speeding up towards the end and was audible only within 40 m of the bird. The following song heard during courtship at 13:45–13:50 on 6 March was typical: "Chit-chit chit-d chit-ter chit (pause) chit-ter chit-ter chit-ter."

"*Chit-Chit*" *call.*—One to many notes; usually two repeated. Frequently given by male or female during construction of both nests and on three occasions by the male during the chick stage at nest #2 when he accompanied the female on recess. On three occasions on 10 and 12 May, the male gave chit-chit calls shortly before the female left the nest to join him. The female gave soft chit-chit calls as he approached nest #2 on 20, 21 May.

Chit notes.—Single "chit" notes were given by parents while foraging together, perhaps as an interspecific flocking call, similar to that of Maui Alauahio.

Alarm call.—During the nestling stage on 2 April at 16:32, the male gave a series of three-noted calls, "chit, chit, chit," interspersed between bouts by single "chit" notes. He was seen perched low in a *Myrsine* sp. tree, while the female brooded. Observers wrote that he "was most likely disturbed by something and giving vocalizations to ward it off," and they implied that the something may have been a small mammal.

Whistle call.—Given once (7 April) by the male foraging in heavy rain

in the vicinity of the brooding female at nest #1 and given on four occasions (14 April) by the male during construction stage of nest #2.

Chatter.—Once during the egg stage at nest #1, the female gave four note chatter while wing-quivering and being fed by the male 1.5 m from the nest. Another observer believed that the male gave the chatter call during feeding.

Nestling calls.—These, if any, were inaudible from the observation points. On the day the successful chick fledged, it gave single, infrequent chit notes when alone on the nest.

Fledgling calls.—We heard none. Reynolds and Snetsinger (pers. comm.) described the calls of a juvenile Poo-uli being fed on 30 August 1994 as "a high-pitched rapid twitter very similar to that of a juvenile Hawaii Creeper (*Oreomystis mana*) or Hawaii Akepa (*Loxops coccineus coccineus*) being fed."

Mechanical sounds.—None. Flight was silent, lacking the wing-whir of some other Hawaiian honeycreepers.

DISCUSSION

Nest site.—The two nest sites we studied are important from both an evolutionary and conservation perspective. Why did the Poo-uli build their nests in tall ohia lehua? Poo-uli forage in the understory and subcanopy at a modal height of 5 m (Mountainspring et al. 1990); the two nests at 8 m were at the high end of their reported foraging range. Even more puzzling, why do the other six species of honeycreepers in Maui rain forests also nest almost exclusively in canopy ohia lehua? Given (1) the diversity in morphology, behavior, and life history traits evolved by the Hawaiian honeycreepers (Amadon 1950, Freed et al. 1987) and (2) the diversity of nest sites used by continental fringillids (Bent et al. 1968, Newton 1972) and passerine communities generally (Martin 1988), the uniformity in nest site selection by rain forest drepanidines is unexpected. While it is beyond the scope of our paper to explore this convergence in the selection of nest sites, we call attention to historic changes in predation pressure on nesting birds in Hawaii. Prior to human settlement, all potential nest predators in these insular forests were birds—rallids, ibises, raptors, owls, corvids, and drepanidines. Nearly all have vanished from Maui forests, and instead six species of small mammals have invaded—a mongoose (*Herpestes auropunctatus*), a cat (*Felis catus*), and four rodents (*Mus musculus, Rattus exulans, R. norvegicus, R. rattus*). Most honeycreeper species have become extinct as direct and indirect consequence of human settlement, including mammalian predation; the surviving species may be nesting in sites relatively safe from the new predators.

Breeding system and parental care.—We have no evidence to show

that the Poo-uli defended an all-purpose territory, as no other conspecifics were seen during the study, and the male did not sing to advertise a territory. Nor did either parent consistently defend the nests from approach by other species. Sightings of the parents foraging in the vicinity of the nest, their relatively weak flight, and the absence of long flights over the canopy suggest that the pair may have confined their activity to a home range of only a few hundred meters in radius.

Even with a sample size of one pair, we are tempted to infer that Poo-uli are principally monogamous, because of the heavy involvement of the male at all stages of the nesting cycle. Pair-bonding extends at least through the breeding season, for the pair initiated the second nest with minimal courtship and no singing. The pair bond may have been reinforced by the male feeding the female regularly throughout both nesting cycles and by the pair consorting during the female's recesses from the nest. Monogamy is universal among drepanidines studied to date (Eddinger 1970; van Riper 1980, 1987; Pletschet and Kelly 1990; Morin 1992; H. Baker and P. Baker, pers. comm.; T. Pratt, unpubl. data; J. Simon, pers. comm., E. van Gelder, pers. comm.) and carduelines generally (Newton 1972).

Parental care by the male and female resembled that of nine other drepanidines studied to date and of carduelines generally (Eddinger 1970; Newton 1972; van Riper 1980, 1987; Pletschet and Kelly 1990; Morin 1992; H. Baker and P. Baker, pers. comm.; T. Pratt, unpubl. data; J. Simon, pers. comm.; E. van Gelder, pers. comm.). We note the likely increase of care-giving to older chicks by the male, documented in few other drepanidines (Morin 1992), but perhaps common. Both parents performed nest sanitation throughout the nestling phase, and we found the successful nest #2 clean of feces. Among drepanidines studied to date (Eddinger 1970; Newton 1972; van Riper 1980, 1987; Pletschet and Kelly 1990; Morin 1992; H. Baker and P. Baker, pers. comm.; T. Pratt, unpubl. data; J. Simon, pers. comm.; van Gelder, pers. comm.), only the Laysan Finch (*Telespiza cantans*) and Palila (*Loxioides bailleui*) give up nest sanitation in the final week of the nestling stage, allowing the rim of the nest to become heavily encrusted with feces. Complete (or nearly complete) nest sanitation by the Poo-uli and other drepanidines that feed their young principally on invertebrate rather than plant foods is presumably a derived behavior, as other carduelines are less fastidious (Newton 1972). The seasonal span of the two Poo-uli nests coincides with peak nesting for most other drepanidines in Maui rainforests (H. Baker and P. Baker, pers. comm.; J. Simon, pers. comm.; E. van Gelder, pers. comm.) and on other islands (Eddinger 1970, Ralph and Fancy 1994).

The male Poo-uli's role of provisioning food to the nesting female and

to his chicks assumes added importance in climatic conditions on the species' relictual geographic range. New weather stations in Poo-uli habitat have recorded annual rainfall ranging from 5–12 m (L. Loope, pers. comm.). Here, trade wind showers can prevail for weeks. Poor weather can threaten the eggs and chicks with hypothermia and pit the survival of progeny against that of parents faced with constraints on foraging time (Drent 1975). Poor weather delayed the female Poo-uli from leaving the nest and curtailed her recesses for foraging. Reduced foraging by the female may have been compensated with provisioning by the male who continued to feed the female on the nest at the same rate (feeding bouts per time spent by the female on the nest) in poor weather as in good. However, the rate at which parents fed the young chick decreased from good to poor weather. We note the greater importance of wind versus rain in influencing the female Poo-uli's time on and off the nest. Wind can have a severe effect on egg temperature, incubation, and incubation behavior in small passerines (e.g., Morton and Pereyra 1985). However, we believe that rain could have had a much greater effect on parental behavior than measured by us. Heavy rains prevented us from observing the nests, and this biased our sampling to "drier" conditions. For example, we were unable to observe nest #1 through the curtain of rain that may have caused its failure. Lastly, Cartar and Montgomerie (1987) found that for female White-rumped Sandpipers (*Calidris fuscicollis*) incubation "behavior appears at least to integrate the effects of both present weather and weather on the previous day." We could not explore such effects with the Poo-uli because of our small data set.

Skutch (1976) noted that time spent on the nest was greater for species in which the incubating bird received food from its mate. He also pointed out the influence of rain on nesting birds. The slower growth rates of chicks of tropical birds has been attributed to food limitation via reduced rate of food delivery by parents (Ricklefs 1976, Martin 1987). The adaptive advantage of monogamous male birds provisioning their mate and young in windy and/or high rainfall environments has received little attention.

Chick development.—The nestling period of 21 days for our Poo-uli chick is intermediate between 15–21 days for Common Amakihi (van Riper 1987) and 22–26 days and 23–29 for Laysan Finch (Morin 1992) and Palila (van Riper 1980; Pletschet and Kelly 1990; T. Pratt, unpubl. data), respectively. At 25.5 g (N = 1; Engilis et al. 1996), the mass of the Poo-uli is greater than that of the Common Amakihi but smaller than that of the Laysan Finch and Palila, suggesting an intermediate nestling period. Nestlings of European cardueline finches that nest in low bushes spend fewer days in the nest and leave at an earlier stage of development

than do nestlings of carduelines nesting in tall shrubs and trees (Newton 1972). Newton (1972) considered early fledging as an adaptation mitigating greater risk to predation. Nestling stage for all four drepanidines is longer than that for shrub- or tree-nesting carduelines (Newton 1972). However, the drepanidine chicks fledged at an advanced stage of development, capable of level flight for short distances and with flight feathers and body size close to that of an adult (van Riper 1980, 1987; Pletschet and Kelly 1990; Morin 1992; T. Pratt, unpubl. data). These differences in fledging time and development indicate an advantage for a prolonged nestling period for the Poo-uli, and perhaps other drepanidines in montane Hawaiian ecosystems.

The second chick apparently hatched two days after the first chick, suggesting hatching asynchrony. The smaller chick died before the larger one fledged, suggesting brood reduction. Whether this is a pattern for second clutches in Poo-uli remains to be determined. Hatching asynchrony and brood reduction occur in Common Amakihi, Laysan Finch, and Palila (van Riper 1987; Pletschet and Kelly 1990; Morin 1992; T. Pratt, unpubl. data).

Diet.—Data on Poo-uli diet are few and tantalizing. Baldwin and Casey (1983), after painstaking analysis of stomach contents of the only two specimens, proposed that Poo-uli feed primarily on various small native lands snails (especially Succineidae), beetles, and proportionately few other arthropods. Mountainspring et al. (1990) reported observations of Poo-uli feeding on insect larvae and succineid snails; they postulated that insect larvae might be a dietary component more important than proposed by Baldwin and Casey. If our data are representative, which they may not be because of observational bias, we confirm that Poo-uli feed extensively on succineid snails. However, we observed lepidoptera and coleoptera larvae being fed to nestlings at any age in greater proportion than succineid snails. Poo-uli appear to conform with most passerines by feeding caterpillars and other insect larvae to their young.

Vocalizations.—Our data, corroborated by observations of others (Mountainspring et al. 1990), show Poo-uli to be the quietest of all drepanidines. We heard the male sing only during courtship and construction at nest #1. At the time of our study, Poo-uli densities were very low, and we did not observe this focal pair interacting with conspecifics. How greater population densities and encounters among birds affected rates of vocalizations is unknown. The song and chit-chit call are both diagnostic and useful for detecting Poo-uli. However, the species' rarity and infrequent vocalizing render conventional censusing ineffective (Scott et al. 1986).

Implications for recovery.—We found nothing in the nesting biology

of this pair of Poo-uli to indicate problems for reproduction or population recruitment. Of significance may be the birds' placing their nests in the foliage of tall ohia lehua trees. We presume this location to be less hazardous than sites in tree cavities, subcanopy trees and shrubs, or near or on the ground, where nests might be encountered more often by non-native, mammalian nest predators. We observed *Rattus rattus* below the nest tree. This notorious enemy of insular birds (Atkinson 1985) thrives in high population density in the study area (Sugihara, in press). Whether the nest sites we observed are typical remains to be determined. Other factors that may help prevent detection of Poo-uli nests by mammalian predators are (1) complete nest sanitation; (2) the absence of odor at the nests, relative to other drepanidine nests (Pratt 1992); and (3) infrequent vocalizations at the nest. Nevertheless, we emphasize that reduction of small mammal populations is crucial to lessening the threat of nest predation for the Poo-uli (Kepler et al. 1984).

The long nestling period and the potential of no more than two young fledging would seem to handicap Poo-uli. However, Maui Alauahio and Maui Parrotbill (*Pseudonestor xanthophrys*), two other sympatric insectivorous honeycreepers sharing these life history characteristics and the same windy and rainy habitat, have far larger geographic ranges and population sizes. We suspect that factors such as decreasing food availability, habitat disturbance by feral pigs, and predation by non-native mammals may be more important to the Poo-uli's decline than vulnerability arising from the species' nesting behavior.

ACKNOWLEDGMENTS

We thank the Hawaii Dept. of Land and Natural Resources, U.S. Fish and Wildlife Service, National Park Service, and The Nature Conservancy of Hawaii for supporting our study and for aggressively pursuing restoration of the Poo-uli; Tom Hauptman for many memorable helicopter flights; Allen Allison, Patrick Ching, Betsy Harrison-Gagne, Larry Katahira, Jim Krakowsky, Joan Suther, and Rick Vetter for assistance with nest observations; Phil Bruner and Allen Allison for collecting inactive Poo-uli nests; John Simon, Michelle Reynolds, and Tom Snetsinger for sharing their observations on Poo-uli; Cheryl Tarr and Rob Fleischer for sharing preliminary findings on molecular evolution in Poo-uli; Allen Allison, Carla Kishinami, and staff at Bishop Museum for facilitating research at their collection; Kim Berlin for discussions and guidance on avian incubation; Greg Brenner, Steve Fancy, and Jeff Hatfield for statistical guidance; Paul and Helen Baker, Tonnie Casey, Fern Duvall, Jr., Steve Fancy, Jeff Hatfield, Marie Morin, and Jim Jacobi for review and discussion of drafts of this paper.

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Wilson Bull., 108(4), 1996, pp. 639–649

POPULATION DENSITY, VOCAL BEHAVIOR, AND RECOMMENDED SURVEY METHODS FOR BICKNELL'S THRUSH

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ABSTRACT.—We studied territorial and vocal behavior of Bicknell's Thrushes (*Catharus bicknelli*) on Mt. Mansfield, Vermont, during June to September 1992 and in June 1993 to 1995. Birds sang and called consistently throughout the day during early–mid June. Later in the season, songs were given infrequently, with vocalizations (mostly call notes) being concentrated at dawn and dusk. Spot-mapping of vocalizing males yielded breeding density estimates of 36–52 pairs/40 ha in 1992, 50–59 pairs/40 ha in 1993, 55–65 pairs/40 ha in 1994, and 45–53 pairs/40 ha in 1995. Other less labor-intensive techniques, including fixed-width point counts and fixed-width transects, generally resulted in lower density estimates. We recommend that future presence-absence surveys for Bicknell's Thrush in the northeastern United States be concentrated from 1–20 June. Surveys from late June through mid-September should be attempted only if observers are able to be on-site before dawn or after sunset. *Received 26 Jan. 1996, accepted 8 May 1996.*

Bicknell's Thrush (*Catharus bicknelli*), recently classified as a distinct species from the Gray-cheeked Thrush (*Catharus minimus*) (Ouellet 1993, American Ornithologists' Union 1995), historically nested from the Gulf of St. Lawrence, Gaspé Peninsula, Magdalen Islands, and Nova Scotia south to the mountains of New England and New York (Wallace 1939). Recent studies have suggested that the breeding range of this bird has been reduced in both the United States and Canada (Ouellet 1993; Atwood et al. 1996; J. Marshall, pers. comm.). The breeding habitat of Bicknell's Thrush consists predominantly of dense, stunted coniferous forest dominated by balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) (Wallace 1939, Atwood et al. 1996). In the northeastern United States, this vegetation type is restricted to mountaintops higher than approximately 915 m elevation (Wallace 1939). Not only are most of these areas somewhat inaccessible geographically, but the habitat itself is difficult to work within, being characterized by nearly impenetrable, dense stands of conifers that are often located on rugged, steep slopes. These logistic challenges have hindered attempts to estimate the current population size of Bicknell's Thrush or to clarify its distributional limits in the United States.

In this study we examine territorial and vocal behavior of Bicknell's

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Thrush in the context of potential techniques that might be used in future population and distributional surveys. In particular, we compare density estimates obtained through labor-intensive spot-mapping of countervocalizing, territorial males (Kendeigh 1944, Robbins 1970, Williams 1936) with estimates derived from fixed-width line transects (Emlen 1974, Kendeigh 1944) and point counts at fixed-radius circular plots (Anderson 1970, Anderson and Shugart 1974). Additionally, we describe studies of the influence of date and time-of-day on Bicknell's Thrush vocal behavior. On the basis of these results, we recommend a standard methodology for future work aimed at assessing the distribution and population status of this poorly known songbird.

METHODS

We established an irregularly-shaped, 8.8 ha study plot on the eastern portion of Mt. Mansfield, Chittenden Co., Vermont (44°32′N, 72°49′W), at approximately 1150 m elevation. Dominant woody vegetation consisted of balsam fir interspersed with limited amounts of red spruce, white birch (*Betula papyrifera cordifolia*) and mountain ash (*Sorbus* spp.). Boundaries of the plot were determined primarily by topography and the location of two pre-existing trails (Long Trail and Amherst Trail). The eastern edge was defined by a nearly vertical cliff face covered with dense balsam fir forest; the western edge followed a major ridgeline that separated suitable Bicknell's Thrush habitat from extremely stunted (<0.5 m high), "krummholz" vegetation located immediately to the west.

Because the plot's dense vegetation and rugged topography made it extremely difficult to leave the established trail system, we did not establish a standard grid system such as usually forms the basis for spot-mapping studies (Franzreb 1981b). Instead, we used compass bearings and tape measurements to map the locations of known "vantage" points throughout the plot. Compass bearings and distance estimates were then taken from these locations for all Bicknell's Thrushes that were seen or heard; these data were later transferred to a master map of the area.

Spot-mapping was conducted on 12 dates in 1992 (11–18, 27–30 June). To validate our 1992 data and to assess changes in density between years, we also spot-mapped on 8 dates in 1993 (8–10, 16, 17, 23, 24, 29 June), 14 dates in 1994 (5–9, 14–17, 20, 22, 23, 29, 30 June), and 16 dates in 1995 (1, 5–8, 12–14, 16, 19, 20, 22, 23, 27 June). Observations made throughout the day were used to estimate the number of territorial males, here assumed to represent breeding pairs. Only the locations of stationary birds were included. Simultaneous registration of two or more vocalizing birds was used as the primary basis for discrimination between adjacent individuals (Robbins 1970). We mapped positions of both singing and calling thrushes, because our observations showed that both types of vocalization were used to indicate territorial status. Although we obtained evidence of occasional calling by females, we are confident that the great majority of calls registered in each year were given by males.

To assess the utility of other less labor-intensive methods for estimating breeding densities of Bicknell's Thrush, we conducted fixed-width line transects and point counts made at fixed-radius circular plots on 10 dates (11–13, 15–18, 27–29 June) in 1992. Transects and point counts, each of which required approximately 1 h to complete, were simultaneously conducted three times per day: morning (beginning approximately 1 hour after sunrise), mid-day (beginning approximately 8 h after sunrise), and evening (beginning approximately 30 min before sunset). Only spot-mapping data from 1992 were used to compare with other census techniques.

The transect line, approximately 1.1 km in total length, followed existing trails that passed through the study plot and formed its western boundary. A single observer walked slowly along the transect and recorded all Bicknell's Thrushes that were seen or heard within 30 m on either side of the trail. No recorded calls or "spishing" were used to elicit responses. The extremely stunted vegetation immediately west of the study plot's western border was deemed unsuitable for Bicknell's Thrushes; consequently, this section of the transect (0.5 km in length) was limited to a strip only 30 m wide, located entirely east of the transect line. A total of 5.1 ha were included in the area sampled by the fixed-width line transect method.

A total of seven 30-m radius circular plots ≥100 m apart were also located in the study area. The positions of these plots were determined by trail and terrain considerations and not by vegetation characteristics or observations of Bicknell's Thrushes. Boundaries of circular plots were marked with flagging tape. A single observer recorded all Bicknell's Thrushes heard or seen during a 5-min period at each plot; recorded calls or "spishing" were not used to elicit vocalization. This basic technique was modified on four dates (11, 15, 18, 27 June) to include the use of recorded playbacks as a means of eliciting Bicknell's Thrush response. After completion of a standard 5-min count, a second count of 5-min duration was conducted in which a tape recording of calls and songs was played for the initial 3 min. A total of 2.0 ha were included in the area sampled by the circular plot method.

To examine the effects of date and time-of-day on Bicknell's Thrush vocal behavior, counts of all songs and calls heard during 5-min periods were recorded at 30-min intervals on 14 dates (11–13, 15–18, 27–29 June; 6, 14, 29 July; 16 September) in 1992. The first of these counts on each date occurred approximately 20 min before sunrise; the last approximately 90 min after sunset. Vocalization counts were conducted near the "Octagon" on Mt. Mansfield (elevation approximately 950 m); 7–10 Bicknell's Thrush territories were estimated to be within hearing distance of this site.

RESULTS

Density estimates.—Spot-mapping of vocalizing males yielded density estimates for Bicknell's Thrush of 36–52 pairs/40 ha in 1992, 50–59 pairs/40 ha in 1993, 55–65 pairs/40 ha in 1994, and 45–53 pairs/40 ha in 1995. The territories of 8, 11, 12, and 10 pairs were located entirely within the borders of the plot in 1992, 1993, 1994, and 1995, respectively. The total number of territories on the plot was estimated at 11.5 in 1992, 13.0 in 1993, 14.25 in 1994, and 11.75 in 1995. Independent evaluation of our data by an individual experienced in spot-mapping but unfamiliar with the plot yielded estimated totals of 11.75 territories in 1992, 13.25 territories in 1993, 12.5 territories in 1994, and 10.0 territories in 1995. Maximum density values were obtained by including percentages of territories estimated to be located within the boundaries of the study plot. Minimum density values were calculated by excluding all "partial" territories from consideration.

Mean densities calculated from point counts conducted without playback elicitation were consistently lower than the maximum estimate derived from spot-mapping but were comparable to the results of spot-mapping when edge territories were excluded (Table 1). Mean values obtained

TABLE 1

DENSITY ESTIMATES FOR BREEDING BICKNELL'S THRUSHES BASED ON CIRCULAR PLOTS AND LINE TRANSECTS

Survey technique	Time of day		
	Morning	Mid-day	Evening
Circular plots (no playback) (N = 10)	36 ± 28.4[a]	8 ± 13.9	32 ± 25.6
	65–97%[b]	15–22%	58–86%
Circular plots (with playback) (N = 4)	48 ± 23.3	66 ± 78.2	35 ± 19.6
	87–130%	120–178%	64–95%
Line transects (N = 10)	23 ± 14.1	5 ± 7.4	18 ± 11.7
	42–62%	9–14%	33–49%

[a] Mean density (pairs/40 ha) ± 1 SD.
[b] Mean density expressed as percent of estimates calculated from spot-mapping results (37–55 pairs/40 ha).

in the morning (36 pairs/40 ha) were slightly higher than those obtained in the evening (32 pairs/40 ha). Mean mid-day results (8 pairs/40 ha) greatly underestimated densities calculated through spot-mapping. The modal density obtained for both morning and evening point counts over the 10 days of the study was 20 pairs/40 ha. Bicknell's Thrushes were not detected within any of the circular study plots during 10% of morning counts, 70% of mid-day counts, and 20% of evening counts.

Use of playback recordings increased the density estimates obtained through point counts, but, in general, the results were still less than the maximum estimate derived through spot-mapping (Table 1). Morning and evening counts resulted in mean density estimates of 48 pairs/40 ha and 35 pairs/40 ha, respectively. Because of a single count in which playback recordings stimulated an unusually large number of territorial interactions, the mean density estimate based on mid-day counts (66 pairs/40 ha) exceeded the maximum estimate based on spot-mapping. Using playback elicitation, the modal densities obtained on morning and evening counts throughout the study period were 40 pairs/40 ha and 20 pairs/40 ha, respectively. All point counts (morning, mid-day, and evening) that made use of playback recordings successfully detected at least one Bicknell's Thrush on each of the four days surveyed using this technique.

Line transects produced the lowest density estimates (Table 1). Results based on morning transects (23 pairs/40 ha) were higher than those obtained in the evening (18 pairs/40 ha). Transect data collected at mid-day underestimated (5 pairs/40 ha) actual densities as calculated through spot-mapping. Bicknell's Thrushes were not detected on 10% of morning transects, 50% of mid-day transects, and 10% of evening transects.

Vocal behavior.—At the time of our preliminary visit to Mt. Mansfield

on 2 June 1992, Bicknell's Thrushes sang and called frequently throughout the day, although no quantitative data were collected. According to Green Mountain Club summit caretakers stationed on the mountain, singing Bicknell's Thrushes had been evident for at least one week prior to this date. In 1993, 1994, and 1995 several individuals were heard calling sporadically during the mornings of our initial site visits that ranged from 25 to 27 May. During mid-June (11–18 June) 1992, Bicknell's Thrushes called and sang consistently throughout the day, with only 18% of the total vocalizations (N = 7998) being restricted to the first and last 2-h periods of the day (Fig. 1). On 15 June, under full moon conditions, Bicknell's Thrushes were silent from 03:00 until the first song was given at 03:57. Of 238 5-min counts conducted during mid-June between 04:30 and 21:30, we failed to record any Bicknell's Thrush vocalizations in only 25 (10.5%) instances.

By late June (27–29 June) the frequency and consistency of Bicknell's Thrush vocalizations declined sharply, and songs, in particular, were given only rarely (Fig. 1). Of the total vocalizations (N = 807) recorded on these dates, 28% occurred during the first and last 2-h periods of the day. We failed to record a single Bicknell's Thrush vocalization during 60 (58.8%) of 102 5-min counts made during late June.

There appeared to be some resurgence in Bicknell's Thrush vocal activity, including both songs and calls, during July (6, 14, 29 July). Of the total vocalizations (N = 1650) detected on these dates, 31% were given during the first and last 2-h periods of the day (Fig. 1). We failed to record a single Bicknell's Thrush vocalization during 51 (50.0%) of 102 5-min counts made during July.

No vocalization samples were obtained during August. On 16 September, Bicknell's Thrushes called inconsistently, and gave no songs during the sampling periods (Fig. 1). Of the total vocalizations (N = 537) recorded on this date, 20% were given during the first and last 2-h periods of the day. We failed to record any Bicknell's Thrush vocalizations during 15 (51.7%) of 29 5-min counts on 16 September.

DISCUSSION

Surveys for Bicknell's Thrush, aimed at determining presence or absence, or at estimating population size, are hindered by significant logistic challenges. In the United States, known breeding habitat occurs almost exclusively on mountaintops of more than approximately 915 m elevation (Wallace 1939; Atwood et al. 1996). Of over 500 such high elevation sites in New York, Vermont, New Hampshire, Maine and Massachusetts that potentially support Bicknell's Thrush, most are accessible only by hiking, and many lack any established trail system. In addition to its

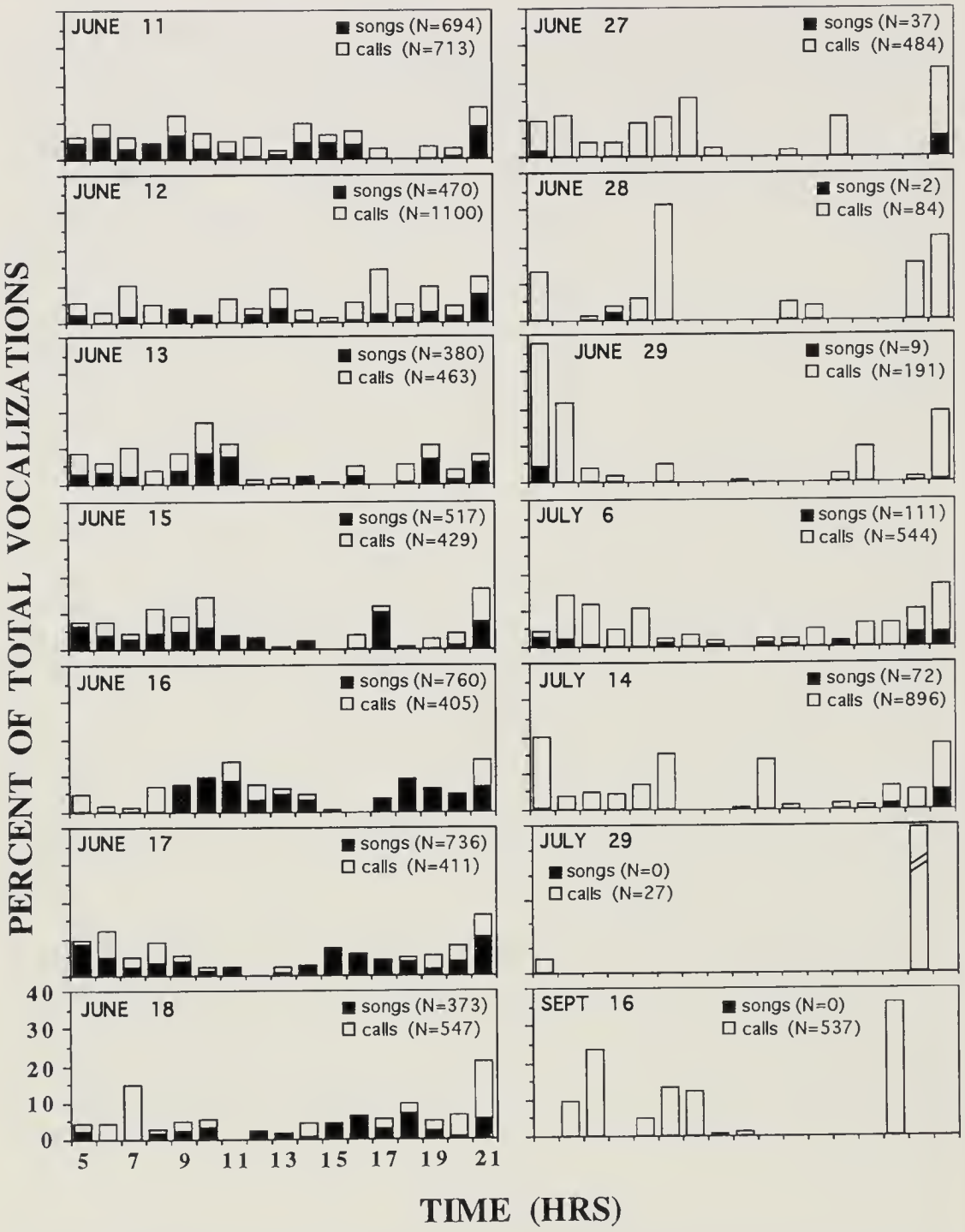

FIG. 1. Daily and seasonal variation in Bicknell's Thrush vocalizations. Axes of all graphs on same scale as shown for 18 June.

frequent occurrence on difficult-to-access peaks, Bicknell's Thrush nesting habitat, which generally consists of nearly impenetrable thickets of stunted coniferous forest located on steep, rugged terrain, is very difficult to work within. Wallace (1939) commented that "only a freak ornithol-

ogist would think of leaving the trails [on Mt. Mansfield] for more than a few feet [due to] the discouragingly dense tangles" of vegetation. Furthermore, the time period in which surveys for Bicknell's Thrush may be effectively conducted is constrained by potentially harsh, high-elevation weather conditions coupled with a brief breeding season. For example, Davenport (1903) described Mt. Mansfield's weather during June 1902 as being "in whole or part rainy . . . with high winds often making it impossible to keep one's footing in the open on the summit."

As a result of our study and data included in Wallace's (1939) classic life history work, we recommend the following protocol for conducting presence-absence surveys for Bicknell's Thrush. Sites in New England and New York should ideally be visited between 1–20 June, during which time songs and calls are consistently given throughout the day. In northern parts of the species' Canadian breeding range, surveys should be conducted several days later than this (Ouellet, pers. comm.). Although Bicknell's Thrush may be present on its United States breeding grounds as early as 17 May (Rimmer and McFarland, unpubl. data), the possibility of northward-bound migrants cannot be excluded until early June (Wallace 1939). Because vocal activity becomes more sporadic later in the season, especially during the middle portion of the day, surveys conducted from late June through mid-September should be attempted only if the observer is able to be present on site at dawn or dusk, and is familiar with the call notes and song of Bicknell's Thrushes. Especially during this time period, we recommend use of playback recordings of songs and calls as a means of eliciting vocal response.

Our vocalization studies failed to show any strong effects of varying weather conditions on singing or calling behavior. Bicknell's Thrushes vocalized consistently in all but the most severe weather during early and mid June. We thus found no evidence to support Wallace's (1939) assertion that "this mist-loving bird has acquired a well-founded reputation for singing more in damp or rainy weather than on clear, sunshiny days." We do, however, recommend that field observers avoid conditions of strong winds (>15–20 knots), moderate to heavy precipitation, and cold temperatures, especially in combination. Under such conditions, Bicknell's Thrush vocalize less frequently, and vocalizations are more difficult to detect.

Although Wallace (1939) suggested that Bicknell's Thrush begins its southward, fall migration in mid to late September, the extent of post-breeding dispersal prior to the onset of actual migration is unknown. At the present time, we tentatively suggest that records obtained in late August and early-mid September in areas of suitable breeding habitat probably represent birds on breeding or natal sites. However, such observa-

tions may also include wandering individuals, and therefore may be of less value as documentation of breeding distribution than records obtained earlier in the summer.

We believe that surveys directed toward actual population censuses of Bicknell's Thrushes throughout their breeding range are impractical, given the extensive areas which must be visited and the difficulties associated with field work on these sites. Instead, we recommend that future population estimates be based on (a) calculation, using satellite or aerial photography, of the extent of suitable habitat, and (b) density estimates obtained from representative sites selected throughout the species' breeding range. We further recommend that a standardized monitoring program be established on a subset of northeastern United States peaks for detection of population trends. This scheme should include sites located throughout the species' range, characterized by varying amounts of subalpine spruce-fir habitat and with differing degrees of isolation from other high elevation areas.

Line transects and point counts both underestimated the densities of Bicknell's Thrushes as compared with the maximum density estimate calculated from spot-mapping of territorial males. Point counts conducted in the morning and evening without playback elicitation yielded results that best approximated the minimum density estimate obtained through spot-mapping. Point counts that made use of playback recordings frequently resulted in inflated density estimates relative to the minimum value obtained through spot-mapping. Our results indicated that fixed-width line transects were the least effective method of estimating the breeding density of Bicknell's Thrushes.

Because we were attempting to evaluate techniques that could provide consistent results even when used by relatively inexperienced observers, we rejected the variable-width transect and variable-width circular plot survey methods that have generally been superior to fixed-width techniques (DeSante 1981; Edwards et al. 1981; Franzreb 1981a, b). Variable-width methods require observers to estimate distances to unseen, vocalizing birds; we found the volume of Bicknell's Thrush vocalizations to be so variable that even trained observers were sometimes unable to estimate accurately distances beyond approximately 30 m. We believe that unlimited distance point counts (e.g., Blondel et al. 1981) provide the most feasible means to obtain abundance indices and assess population trends of Bicknell's Thrushes on a rangewide basis. These types of count eliminate difficulties of distance estimation, are much less labor intensive than spot mapping, and are well suited for use in a single habitat type over multiple years (Blondel et al. 1981).

Based on our field experience with Bicknell's Thrushes, we believe that

use of tape recorded playbacks may increase the efficiency of detecting the species, when present, and may lead to more accurate counts, as suggested for other species by Marion et al. (1981) and Falls (1981). We recommend that future censuses of Bicknell's Thrushes be conducted as standardized series of unlimited distance point counts. Counts at each point should include an initial 5- or 10-min period of listening, followed by a 1-min taped broadcast of songs and calls and an additional 4-min listening period. Thrushes detected during both portions of each point count should be tallied separately, to compare the relative efficiency of both methods and to allow comparability with other censuses that may not employ tapes.

The density estimates we calculated from spot-mapping data on Mt. Mansfield in 1992 to 1995 were higher than those reported from two other similar studies of this species in New Hampshire. Morse (1979) recorded Bicknell's Thrush densities of 22 pairs/40 ha on Mt. Osceola, while Sabo (1980) estimated only 4 pairs/40 ha on Mt. Moosilaukee. However, our data may not be strictly comparable to those of other studies due to differences in sampling frequency and technique (Rimmer, unpubl. data), seasonal timing of censuses (Morse 1979), plot size (Morse 1979, Sabo 1980), and elevational and habitat gradients over which sampling occurred (Morse 1979; Sabo 1980; Rimmer and McFarland, unpubl. data). We believe that our spot-mapping data, from which two independent observers calculated similar numbers of territories in 1992–1995, closely approximated actual Bicknell's Thrush densities on the study plot. Marchant (1981) reported that edge-effects in spot-mapping studies tended to inflate density estimates by incorrectly including 10–27% of "edge clusters" that do not strictly belong to the plot. Discounting 27% of partial territories in this study results in maximum estimates of 48 pairs/40 ha in 1992, 57 pairs/40 ha in 1993, 62 pairs/40 ha in 1994, and 55 pairs/40 ha in 1995. We believe these to be more accurate than our minimum values calculated by excluding all partial territories.

Wallace (1939) reported that Bicknell's Thrush territories on Mt. Mansfield "may apparently cover an acre or more". Assuming densely-packed territories of about 0.6 ha (1.5 ac) in size, Wallace's suggestion would yield density estimates of approximately 65 pairs/40 ha. This is similar to our maximum estimates and may reflect unusually high densities on Mt. Mansfield, which we believe supports >250 pairs. Further study of Bicknell's Thrush territorial behavior, based on observation of color-banded or radio-marked birds, is clearly warranted, as are studies of possible geographic differences in breeding density and habitat selection.

ACKNOWLEDGMENTS

We thank Dan Lambert, Karin Fischer, Andrew Ingersoll, and Jamie Christian for their invaluable field assistance, and Jim Goetz for assistance with data transcription. Rick Paradis

of the University of Vermont, William Kemp and Rob Apple of the Mt. Mansfield Co., and the summit caretakers of the Green Mountain Club all provided logistical support. Trevor Lloyd-Evans independently plotted spot-mapping data for each year. Joe Marshall and Henri Ouellet provided useful discussions of Bicknell's Thrush biology. We thank Henri Ouellet, Walter Ellison, and an anonymous reviewer for helpful comments on the manuscript. This project was supported financially by the U.S. Fish and Wildlife Service, the National Fish and Wildlife Foundation, the William P. Wharton Trust, the Vermont Monitoring Cooperative, and the members and trustees of the Vermont Institute of Natural Science and Manomet Observatory for Conservation Sciences.

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DISTRIBUTION OF BICKNELL'S THRUSH IN NEW ENGLAND AND NEW YORK

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ABSTRACT.—We conducted presence-absence surveys for Bicknell's Thrush (*Catharus bicknelli*) in Marine, Massachusetts, New Hampshire, New York, and Vermont during the 1992–1995 breeding seasons. The species was found at 234 sites, of which 225 (96%) were dominated by varying mixtures of balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*). Ninety-one percent of the occupied sites were ≥915 m (3000 ft) in elevation. Size of occupied habitat patches was generally small; 73% of occupied areas delimited by the 915 m elevation contour were less than 1000 ha in extent. A logistic regression model using independent variables describing vegetation, elevation, land area ≥915 m located within 1 km of a site, and latitude successfully predicted thrush presence. There was no conclusive evidence of widespread population declines of Bicknell's Thrush in the United States; we found the species at 63 of 73 sites (86%) known to have been occupied prior to 1992. However, the restricted breeding distribution and narrow habitat requirements of Bicknell's Thrush in the United States suggest that it is vulnerable to habitat loss and degradation, and that continued efforts to document the species' status and ecology are warranted. *Received 26 Jan. 1996, accepted 18 May 1996.*

Bicknell's Thrush (*Catharus bicknelli*), until recently considered a subspecies of the Gray-cheeked Thrush (*Catharus minimus*) (Ouellet 1993, American Ornithologists' Union 1995), breeds from southern Quebec and the Maritime Provinces south to the higher elevations of New England and New York (Wallace 1939, Ouellet 1993). Suitable nesting habitat of this species in the United States has been described as dense forests of balsam fir (*Abies balsamea*) and red spruce (*Picea rubens*) occurring near tree-line (Wallace 1939). In Canada, the species also occurs at lower elevations, and has been documented in regenerating clearcuts and coastal areas where structure of the spruce-fir habitat approximates that found in the United States at higher elevations (Ouellet 1993; E. Nixon, unpubl. data).

Concern recently has been raised that Bicknell's Thrush has disappeared from portions of its historic range, especially in Canada (J. T. Marshall, pers comm.; E. Nixon, unpubl. data), and various factors seem to pose likely threats to the species. In its breeding range, habitat degradation caused by acid precipitation (Vogelmann 1982, Schreiber and Newman 1988), replacement of high elevation coniferous forests by de-

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ciduous tree species as a result of global warming (Davis and Botkin 1985, Rodenhouse 1991), or habitat loss caused by development of ski resorts or communications facilities could conceivably impact it. On its wintering range, apparently restricted to the Greater Antilles (Wallace 1939, Ouellet 1993), Bicknell's Thrush may be threatened by deforestation (Arendt 1992; Wunderle and Waide 1993; Rimmer and McFarland, unpubl. data).

The Committee on the Status of Endangered Wildlife in Canada currently is considering a proposal to designate the bird as "threatened" in Canada (E. Nixon, unpubl. ms), and in the United States Bicknell's Thrush was listed as a Category 2 candidate species under the Endangered Species Act in 1994 (U.S. Fish and Wildlife Service 1994). Rosenberg and Wells (1995) identified Bicknell's Thrush as the top priority for conservation concern among neotropical migrant birds in the northeastern United States.

Few empirical data exist by which to evaluate the current status of Bicknell's Thrush, and various aspects of the species' life history have caused it to be exceptionally difficult to study (Rimmer et al. 1996). In this paper we present the results of surveys for Bicknell's Thrush conducted in Maine, Massachusetts, New Hampshire, New York, and Vermont from 1992–1995. Where possible, we compare these data with historic distributional information. Finally, we present a preliminary quantitative model for assessing the probability of occurrence of Bicknell's Thrush in the United States portion of its breeding range.

METHODS

We solicited survey volunteers from various sources. Cooperators were instructed to collect data in a standardized manner. Each cooperator was provided with a tape recording of Bicknell's Thrush songs and call notes obtained from the Cornell Laboratory of Ornithology's Library of Natural Sounds. We emphasized censusing at locations where the bird was previously recorded and at areas located above 915 m elevation. Three hundred eighty localities were visited during June and early July 1992–1995, usually within 3 h of sunrise or sunset. Bicknell's Thrush was determined to be present on the basis of clearly identified vocalizations or observation of a territorial bird responding to broadcast tape recordings. Dominant habitat at each site [VEG] was subjectively categorized as (1) spruce-fir forest, (2) mixed hardwood-coniferous forest, or (3) northern hardwood forest. Elevation above sea level at each survey location [ELEV] was approximated to the nearest 100 ft.

Given the limited nature of these surveys and the variable levels of expertise among observers, we cannot certainly conclude that Bicknell's Thrushes were absent from locations where we failed to encounter them, especially at areas that were visited only on a single date (N = 80). However, during 213 visits to sites where Bicknell's Thrushes were known to occur and which were surveyed on two or more dates, the species was missed in only 20 instances (9%), suggesting that when appropriate sampling protocols are used (Rimmer et al. 1996), even single visits are likely to detect the species when it is present.

In addition to these surveys, we also incorporated relevant data collected from 1992–

1995 as part of more intensive studies of bird populations and forest habitats in Maine (35 sites; J. M. Hagan, unpubl. data) and Vermont (15 sites; C. C. Rimmer, unpubl. data). Although these projects did not use playbacks of Bicknell's Thrush vocalizations, nonetheless we believe that the multiple visits made to each site by trained observers familiar with the songs and calls of all local breeding species warrant inclusion of these data in our analysis.

All surveyed localities were manually digitized from 1:24,000 USGS topographic maps using ArcInfo GIS software, as were all 915 m (3000 ft) contour lines in the study region. For each point in the resulting data set, we calculated an index of latitude [LAT], the amount of high elevation land (≥915 m) occurring in a 1-km diameter circle centered on the survey point [KM1], and the amount of high elevation land occurring in a 10 km diameter circle centered on the survey point [KM10]. KM1 was considered to reflect habitat availability in the immediate vicinity of the survey point, while KM10 provided a representation of the survey point's location relative to the regional distribution of high elevation land. Additionally, ArcInfo was used to calculate the area of high elevation polygons, as delineated by the 915 m elevation contour, that were occupied by Bicknell's Thrushes. Area estimates were not corrected for topography.

Using the SAS procedure LOGISTIC, we performed a stepwise logistic regression (Mills et al. 1993, Akçakaya et al. 1995) with the response variable defined as thrush presence (1) or absence (0). Independent variables (VEG, ELEV, LAT, KM1, and KM10) were added and removed at a significance level of $P = 0.05$. A total of 392 sites for which complete and unambiguous data were available were used in this analysis.

We also conducted road-based surveys from 18–21 June 1993 in the north Maine woods from T. 11 R. 17 east to Garfield Township, from T. 11 R. 13 southeast to T. 7 R. 11, and from Garfield Township southwest to T. 9 R. 8. These surveys consisted of 294 5-min stops spaced at intervals of approximately 1 km. Recordings of Bicknell's Thrush vocalizations were broadcast at each point to elicit responses from any birds that might be present. All road-based point surveys were conducted prior to 11:00 under good weather conditions; lakes and recent clear cuts were excluded. However, because data from these surveys were not recorded in a geographically explicit format, we did not include these results in calculating the quantitative habitat suitability function described above.

RESULTS

A total of 430 localities (251 sites >915 m elevation, 87 sites from 610–915 m, 10 sites from 305–610 m, and 82 sites ≤305 m), were surveyed for Bicknell's Thrushes. The species was found at 234 of these sites (Fig. 1). A detailed list of documented sites of its occurrence (through 1995) is available on request from the senior author. The species was found at 234 sites, of which 225 (96%) were dominated by varying mixtures of balsam fir and red spruce. Ninety-one percent of the occupied sites were ≥915 m (3000 ft) in elevation. Road-based surveys in the north Maine woods failed to encounter *bicknelli* at any of 294 point localities.

Ninety-nine high elevation polygons, arbitrarily defined as areas demarcated by the 915 m elevation contour, were occupied by Bicknell's Thrushes. Of these, 73 (74%) were relatively small in size, being characterized by <1000 ha of land ≥915 m elevation (Fig. 2). The mean area of distinct high elevation polygons occupied by *bicknelli* was 1046 ha

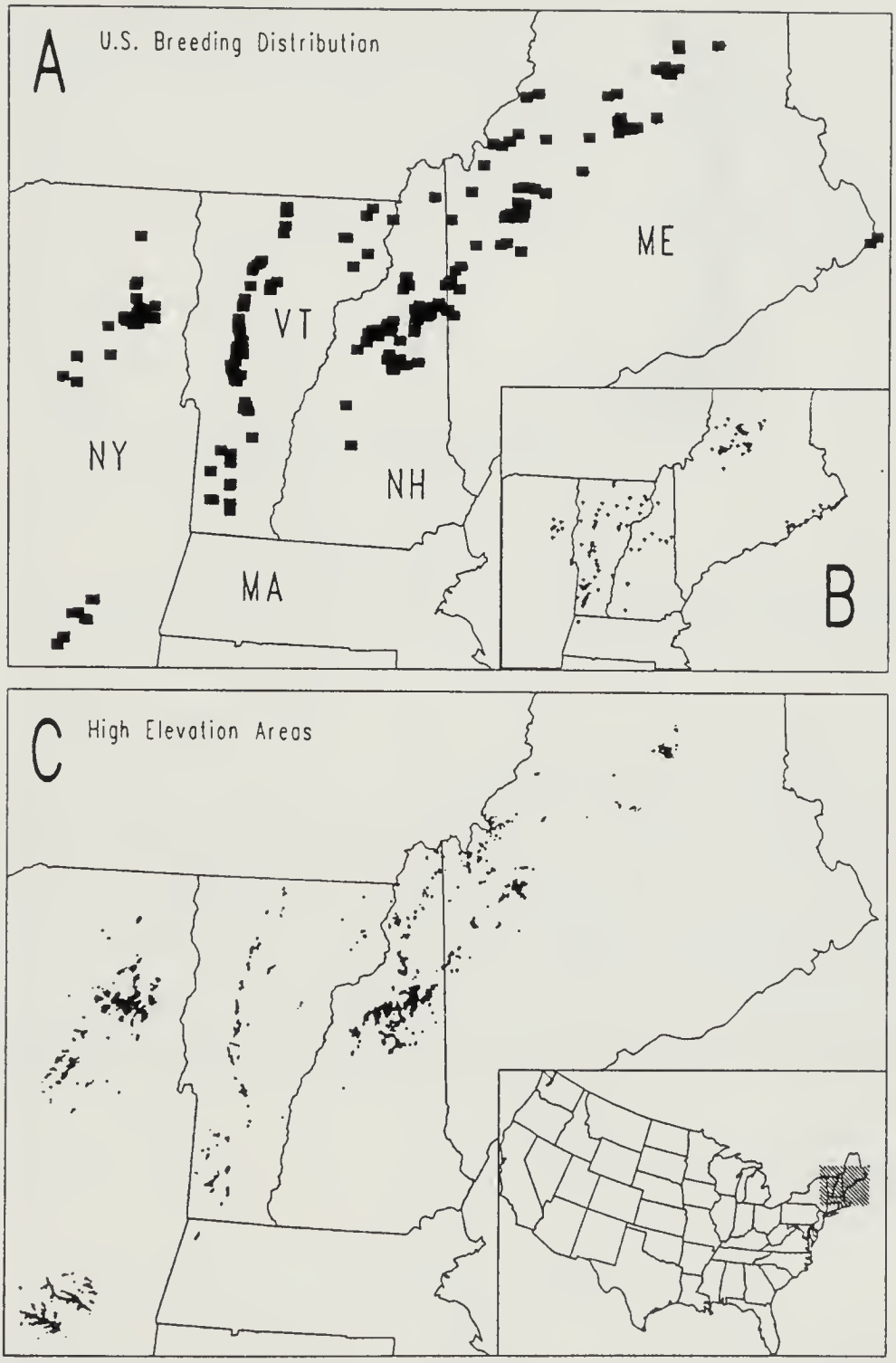

FIG. 1. (A) Documented occurrence of Bicknell's Thrush within its United States breeding range. (B, inset): Sample localities where Bicknell's Thrush was not encountered. (C) Location of high elevation (>approximately 900 m) land in New England and New York.

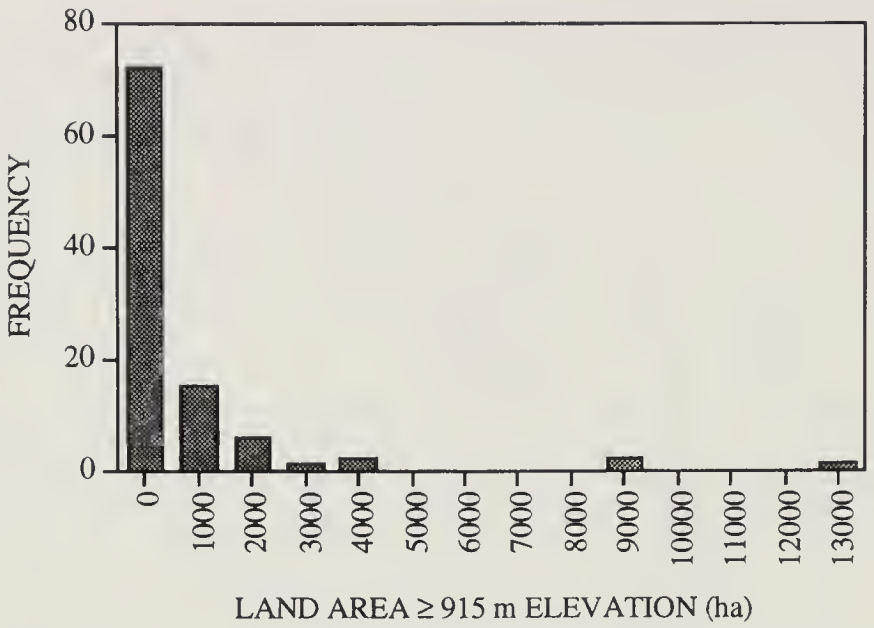

FIG. 2. Frequency distribution of area estimates of high elevation land occupied by Bicknell's Thrush in the United States.

(SD = 2006; range 1.5 ha (Little Bigelow Mtn., Maine)–130,020.1 ha (Mt. Washington, New Hampshire).

Approximately 155,295 ha of land ≥915 m elevation were identified in New England and New York; areas ≥793 m (2600 ft) that were categorized by Miller-Weeks and Smoronk (1993) in vegetation classes likely to be occupied by Bicknell's Thrushes totalled 99,188 ha in western Maine, the Adirondack region of New York, New Hampshire, and Vermont (Table 1). Neither of these values should be construed as actual measurements of the extent of Bicknell's Thrush habitat. Nonetheless, these results do suggest that the maximum land area potentially occupied by the species in the United States is probably in the range of 100,000–150,000 ha.

Stepwise logistic regression yielded the following index of habitat suitablity:

$$P = 1/(1 + \exp(-\beta_0 - (\beta_1 \cdot \mathrm{VEG}) - (\beta_2 \cdot \mathrm{ELEV}) - (\beta_3 \cdot \mathrm{KM1}) - (\beta_4 \cdot \mathrm{LAT}))),$$

where P is the probability of occurrence, VEG, ELEV, KM1, and LAT are the data values from each site, and β_X are the associated regression coefficients (Table 2). Based on the goodness of fit statistics (Chi-square for covariates: log likelihood statistic = 289.8 with 4 df, $P = 0.0001$; score statistic = 221.8 with 4 df, $P = 0.0001$), the model is highly significant. Sites occupied by Bicknell's Thrushes had a mean habitat suit-

TABLE 1

ESTIMATES OF APPROXIMATE MAXIMUM EXTENT OF BICKNELL'S THRUSH HABITAT IN NEW ENGLAND AND NEW YORK

	Area ≥ 915 m (ha)[a]			Area ≥ 793 m (ha)[b]	
	Total	Mean	SD	Spruce-fir	Total sample
Maine					
Western Maine	18,332	168	498	32,366	45,458
Other	6471	196	639	na	0
Massachusetts	302	151	180	na	0
New Hampshire	54,480	436	1572	34,154	88,632
New York					
Catskills	17,305	247	530	na	0
Adirondacks	41,674	344	1050	28,393	79,205
Vermont	16,731	164	359	4275	45,858

[a] Estimates of land area (uncorrected for topography) ≥915 m (3000 ft) elevation.
[b] Estimates of land area ≥793 m (2600 ft) elevation. Spruce-fir estimates based on values for "Spruce-Fir Slope" and "Balsam Fir" categories provided by Miller-Weeks and Smoronk (1993). "Total Sample" = total amount of photographed land area included in analysis by Miller-Weeks and Smoronk. na = data not available.

ability value of 0.831 (SD = 0.19); sites where we failed to document the species had a mean value of 0.221 (SD = 0.29).

However, because these data were used to calculate the habitat function, they cannot be considered an independent validation of the model's predictive power. To validate use of this approach to predict occupancy of a site by Bicknell's Thrushes we randomly subdivided the overall data set into two equal parts (N = 196), recalculated a new habitat suitability function based on one part (A) and then applied the resultant model to the second part (B) of the data. Using this smaller sample size, the variables KM1 and KM10 both failed to meet the stepwise selection criterion,

TABLE 2

RESULTS OF STEPWISE LOGISTIC REGRESSION PREDICTING BICKNELL'S THRUSH PRESENCE IN NEW ENGLAND AND NEW YORK[a]

Variable	Regression coefficient	Standard error	Wald Chi-square	Probability
INTERCEPT	−36.6017	9.4148	15.11	0.0001
ELEV	0.00151	0.000325	21.59	0.0001
VEG	−1.9502	0.4069	22.97	0.0001
LAT	0.00000691	0.00000185	14.16	0.0002
KM1	0.0200	0.00678	8.72	0.0031

[a] Variables listed in order of entry into model. 10KM failed to meet the 0.05 significance level for inclusion.

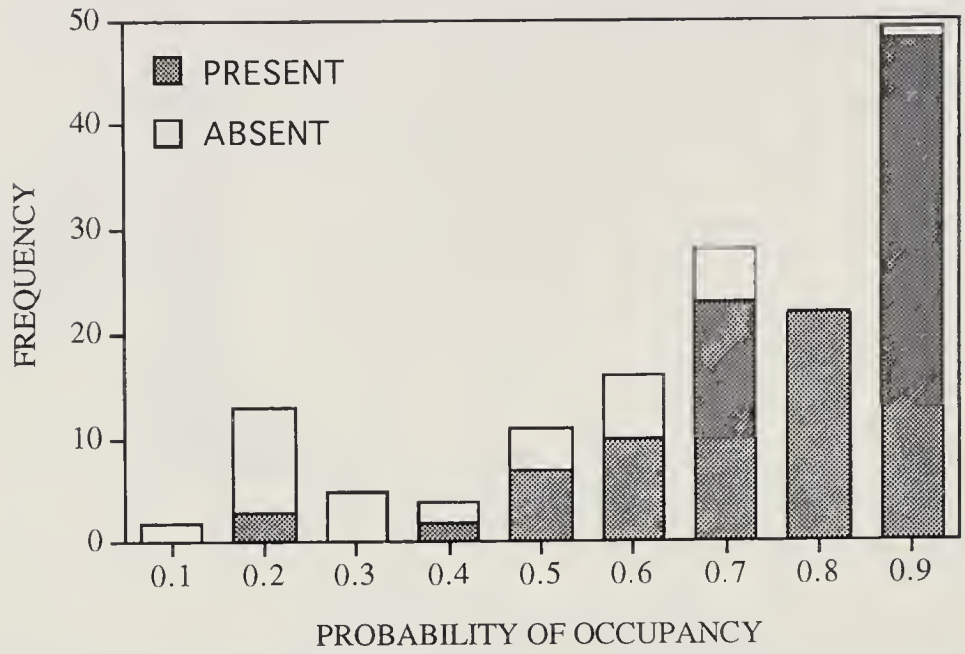

FIG. 3. Frequency distribution of habitat suitability values (probability of occurrence) among subset (N = 196) of total dataset, based on logistic regression model derived from a different data subset (N = 196). Habitat suitability index varies from 0 (no probability of occurrence) to 1 (certain probability of occurrence).

so the model included only ELEV, VEG, and LAT as independent variables. Eighty-nine percent of sites in subset B where Bicknell's Thrushes were observed had predicted occupancy values ≥ 0.60 based on the model derived from data subset A, and 85% of unoccupied sites had values <0.60 (Fig. 3).

Two sites (Quoddy Head State Park and Boot Head, Maine) where Bicknell's Thrushes were reported were poorly accounted for by the overall regression model (Pearson residuals = 7.50 and 7.38, respectively). Both areas are located coastally near sea level and represent the only low elevation sites in the United States where the species was documented during 1992–1995. The sighting from Quoddy Head State Park occurred on 4 Jul 1993; the species was not subsequently seen at this site during multiple visits from 1993–1995. At Boot Head, Bicknell's Thrush was reported on 12 Jun 1993, but later surveys during 1993, as well as multiple visits in 1994 and 1995, failed to locate the species. If correctly identified, the two 1993 records may involve transient rather than breeding individuals.

We found 98 historic (pre-1992) breeding sites for Bicknell's Thrush in Maine, Massachusetts, New Hampshire, New York, and Vermont through literature review and correspondence with active field ornithologists. Seventy-three of these localities were surveyed from 1992–1995;

TABLE 3
SUMMARY OF 1992–1995 BICKNELL'S THRUSH SURVEYS AT HISTORIC (PRE-1992) SITES IN NEW ENGLAND AND NEW YORK

State	Historic sites (total)	Historic sites visited	Present	Absent
Maine	5	5	5	0
Massachusetts	2	2	0	2
New Hampshire	26	20	16	4
New York	33	16	16	0
Vermont	32	30	26	4
TOTAL	98	73	63	10

Bicknell's Thrushes were documented at 63 sites (86%) (Table 3). Historic sites where we failed to find *bicknelli* included: *Massachusetts*—Mt. Greylock (3 visits), Saddleball Mtn. (3 visits); *New Hampshire*—Mt. Pemigewasset (1 visit), Mt. Monadnock (1 visit), Mt. Sunapee (1 visit), and North Moat Mtn. (1 visit); *Vermont*—Glebe Mtn. (Magic Mtn.) (1 visit), Green Peak (Mt. Aelous) (3 visits), Mt. Ascutney (2 visits), and Molly Stark Mtn. (3 visits). At Mt. Greylock, the only historic locality where Bicknell's Thrush numbers have been recorded over an extended period of time (29 years between 1938–1993), population estimates suggest a gradual, long-term decline that culminated in the species' disappearance from the site in 1973 (Fig. 4; Veit and Petersen 1993).

DISCUSSION

In the United States, Bicknell's Thrush regularly breeds only at the higher elevations of Maine (730–1280 m, but see below), New Hampshire (850–1460 m), New York (880–1430 m), and Vermont (820–1250 m). Because its obligate habitat, subalpine spruce-fir forest (Wallace 1939, Rimmer et al. 1996), is generally restricted to mountaintops surrounded by large areas of northern hardwoods or mixed hardwood–conifer stands, the distribution of *bicknelli* in the United States is extremely patchy at the landscape level. Furthermore, of high elevation (≥915 m) regions known to be occupied by the species, few exceed 1000 ha in area, suggesting that much of the range of Bicknell's Thrush in the United States is limited to relatively small fragments of suitable habitat. We did not encounter the species in low elevation, regenerating clearcuts as has been reported in Canada (Ouellet 1993; E. Nixon, unpubl. ms).

The status of Bicknell's Thrush in coastal Maine is problematical. The species has been documented at various low elevation, coastal areas of Quebec (Ouellet 1993, Gauthier and Aubry 1995), New Brunswick (Er-

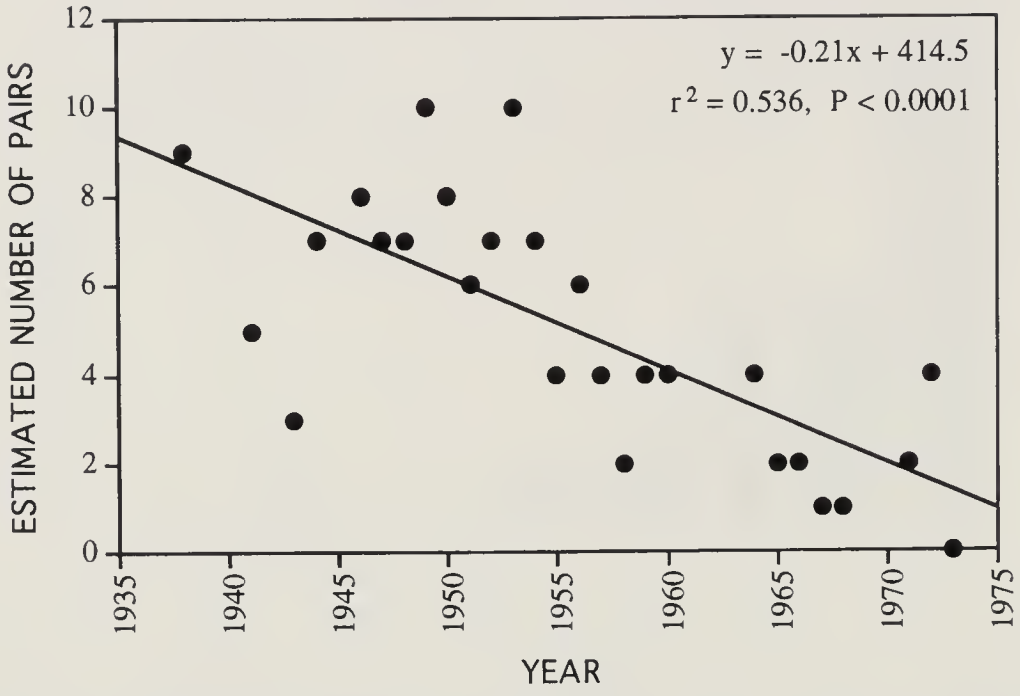

FIG. 4. Decline and local extinction of Bicknell's Thrush on Mt. Greylock, Massachusetts.

skine 1992), Nova Scotia (Allen 1916, Erskine 1992, Wallace 1939), and Prince Edward Island (Erskine 1992), lending credence to the possibility of its breeding in coastal Maine. However, we obtained only two coastal records during our study, and both were at sites where the species could not be confirmed during multiple subsequent visits by experienced observers. Wallace (1939) reported that Gross, Pettingill, and other ornithologists never detected Bicknell's Thrush during their intensive studies of the avifauna of coastal Maine. At the present time, we do not feel that available data warrant inclusion of coastal Maine within the breeding range of Bicknell's Thrush, although more field work in this area is certainly desirable.

Lack of detailed historic data makes it difficult to evaluate whether populations of *bicknelli* in the United States have declined in recent years. The species has disappeared from its principal site of historic occurrence in Massachusetts (Mt. Greylock), where the population numbered approximately 5–10 pairs in the early 1900s. Based solely on presence-absence determinations, we found no clear evidence that Bicknell's Thrush has declined in Maine, New Hampshire, New York, or Vermont.

However, although these data do not substantiate recent concerns that Bicknell's Thrushes may be showing serious rangewide declines in the United States, neither have we refuted this possibility. We believe that the distribution and ecology of the species places it in a precarious po-

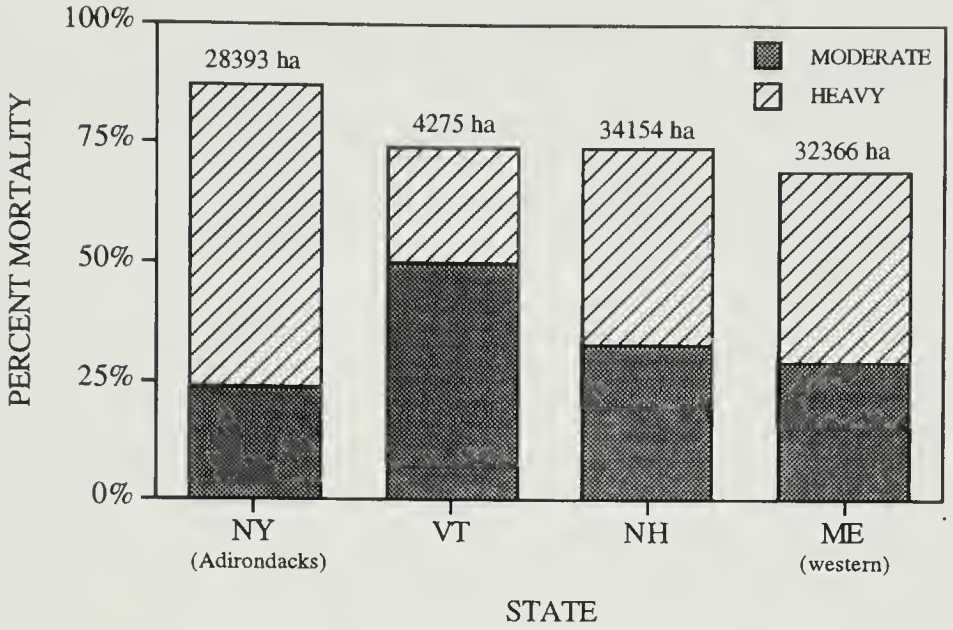

FIG. 5. Condition of high elevation (≥793 m) spruce-fir forests occurring in New York's Adirondack region, Vermont, New Hampshire, and western Maine. Based on data presented by Miller-Weeks and Smoronk (1993). Mortality classifications: Moderate = 11–30% standing dead trees; Heavy = >30% standing dead trees. Total area of "Spruce-Fir Slope" and "Balsam Fir" cover types occurring at elevations ≥793 m (2600 ft) provided above each bar (Miller-Weeks and Smoronk 1993).

sition that warrants further monitoring efforts. Acid precipitation, global warming, and other complex biotic and abiotic factors have been postulated as potentially impacting the geographically limited, high elevation spruce-fir ecosystem (Weiss and Millers 1988) that is required by Bicknell's Thrushes breeding in the United States. In fact, Miller-Weeks and Smoronk (1993) found, based on data collected 1985–1986, that most areas of high elevation spruce-fir habitat in New England and the Adirondack region of New York showed extensive levels of tree mortality (Fig. 5). The causes of this spruce-fir mortality are uncertain, and no information is available concerning its possible impacts on the biology of Bicknell's Thrushes or other birds that breed at high elevations. Finally, if the species' poorly-known wintering grounds are, in fact, restricted to the Carribean (Wallace 1939, Ouellet 1993), then the extensive deforestation that has occurred in this region (Arendt 1992; Rimmer and McFarland, unpubl. data) would also be expected to adversely impact the population.

Based on these reasonably postulated threats, Bicknell's Thrush should be ranked as one of the most potentially threatened species of Neotropical migrant songbirds in the United States (Reed 1989, Rosenberg and Wells 1995). Further research should attempt to clarify details of its current

breeding and wintering distribution, calculate population sizes based on remote sensing data combined with regionally-explicit density estimates, evaluate levels of population interchange among birds breeding on isolated mountain peaks, and assess the impacts of differences in habitat quality on Bicknell's Thrush occupancy and reproductive success.

ACKNOWLEDGMENTS

We especially thank the many survey and data entry volunteers who contributed their time and energy. Although too many to list individually, this project would have been impossible without their help. C. Darmstadt, R. Harrison, T. Nunan, W. Richardson, D. North, and N. Famous all contributed field assistance. J. Marshall and H. Ouellet provided useful discussion of Bicknell's Thrush biology. Environmental Systems Research Institute, Inc. provided ArcInfo and ArcView GIS software, and Stacie Grove patiently explained its intricacies. This project was supported financially by the U.S. Fish and Wildlife Service, the National Fish and Wildlife Foundation, the Wharton Trust, the Plumsock Fund, and the trustees and members of Manomet Observatory for Conservation Sciences and the Vermont Institute of Natural Science.

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Wilson Bull., 108(4), 1996, pp. 662–672

MIGRATION ROUTES OF THE WESTERN SANDPIPER

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Abstract.—We report the locations of 97 sightings of over 15,000 Western Sandpipers (*Calidris mauri*) color banded in Perú, Panamá, México, British Columbia, and Alaska. Ninety-five sightings were made in states and provinces along the Pacific Coast of Central America and North America. One sandpiper banded in British Columbia and one from Perú were seen east of the Rocky Mountains. We propose that most Western Sandpipers migrate from Central and South American winter quarters along the Pacific Coast of North America. We also propose that most post-breeding Western Sandpipers use a trans-Pacific route that bypasses southeast Alaska and makes landfall in southern British Columbia. Western Sandpipers that spend the winter on the Atlantic coast of the USA and in the Caribbean fly a trans-continental route beginning from the Pacific Coast of North America. *Received 27 Sept. 1995, accepted 1 April 1996.*

Most Arctic breeding shorebirds stop at several staging sites to rest and feed while migrating to and from their winter quarters. A generally held view is that staging sites contribute to the reproductive fitness of individual shorebirds (Davidson and Evans 1988, Alerstam and Lindstrom 1990, Ens et al. 1994) and the degradation of these sites will result in population declines (Davidson and Evans 1986, Davidson and Piersma 1992). As a beginning, an assessment of this hypothesis requires a description of migratory routes. For even the most abundant shorebird species, however, migratory routes and staging sites are not well known (Morrison 1984).

The Western Sandpiper (*Calidris mauri*) is the most numerous shorebird on the Pacific Coast of North America. Between 250,000 and one million individuals are present on single days in San Francisco Bay, Grays Harbor, the deltas of the Fraser, Stikine, Fox, and Copper rivers, and Redoubt and Kachemak bays during spring migration from mid-April through mid-May (Page et al. 1979, Butler 1994, Gill et al. 1994, O'Reilly and Wingfield 1995). Single-day counts at these sites are 10- to 15-fold smaller during the southward migration from late June to mid-September (Senner 1977, Page et al. 1979, Butler 1994). Radio-tagging studies by Iverson et al. (1996) confirmed that many of the same individuals used

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these sites during spring migration. Despite its abundance, the migratory pathways of the Western Sandpiper are incompletely known. It is clear that most Western Sandpipers migrate along the Pacific Coast of the United States and Canada (Gill 1979, Gill et al. 1994). Senner and Martinez (1982) used data from regional bird accounts and recoveries of banded birds to postulate that a small number of Western Sandpipers use an interior route through the Great Plains east of the Rocky mountains to and from Alaska's North Slope and that some Western Sandpipers travel north in spring along the Pacific Coast and return to wintering quarters by routes that cross portions of the continental interior. Migration routes south of the United States of America were not described.

The purpose of this paper is to report sightings of banded Western Sandpipers in the Americas up to February 1996 and to relate them to migration routes proposed by Senner and Martinez (1982).

STUDY AREAS AND METHODS

Perú, Panamá, and México represent the respective southern, central, and northern portions of the winter range of the Western Sandpiper on the Pacific Coast of the Americas (American Ornithologists' Union 1983), whereas British Columbia is a staging site used by large numbers of Western Sandpipers in spring and autumn (Butler et al. 1987, Butler 1994). Most Western Sandpipers were captured in mist nets and fitted with colored darvic plastic "flag" bands to the legs at Paracas near Pisco, Perú (13°42′S, 76°13′W), near Chitré, Republic of Panamá (7°58′N, 80°26′W), near Ensenada, México (31°52′N, 116°37′W), on Sidney Island, BC (48°40′N, 123°30′W), and at Safety Sound near Nome, AK (64°20′N, 164°56′W) (Figs. 1, 2).

About 300 Western Sandpipers were banded with yellow flags in Perú between December 1990 and May 1991, about 14,000 were banded with red over white flags in Panamá between January 1989 and April 1995, 100 were banded with red over yellow flags in México in February and March 1993, 553 were banded with white flags in British Columbia in July and August 1990–1994, and 1271 were banded with green flags in Alaska in June and July 1994–1995. We relied on birdwatchers and biologists to send us sightings of banded birds, which created a bias in the reporting locations since sighting rates will depend on the intensity of search. Ten juveniles had miniature (0.8 g) radio transmitters glued to the feathers of the back (Warnock and Warnock 1993) near Nome, Alaska on 11 July 1994. Daily scans with a hand-held Yagi antenna and radio receiver were made every kilometer along dykes near the high tide line on the Fraser River delta, British Columbia from 14 July to 10 August 1994. The search area was along Boundary Bay and southern Roberts Bank where large numbers of Western Sandpipers roost during high tide (Butler 1994).

There is the possibility that some birds that lost a flag were identified with the wrong country. We received two reports of birds with only red flags out of about 14,000 that were banded. Red flags are the designated color for Chile where Western Sandpipers are very rare (Modinger et al. 1986), and none has been banded (M. Sallaberry, pers. comm.). These also could have been Mexican-banded sandpipers that lost a yellow flag. Sightings of yellow flags from Perú were made before red and yellow flags were used in México. Some white flags attached to sandpipers in Panamá had become stained yellow when the birds were recaptured a few years later. All birds in Canada were banded with white flags and colored

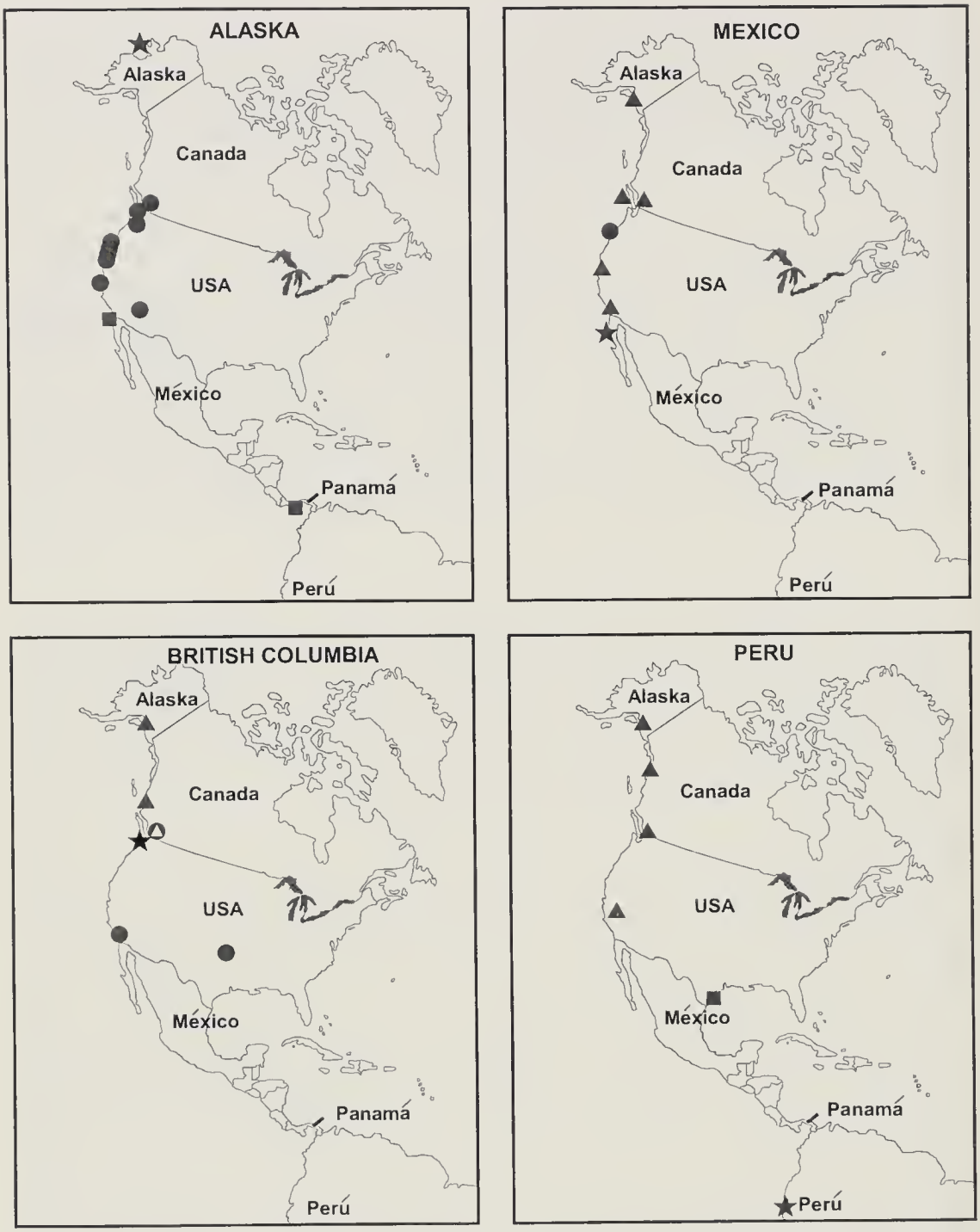

FIG. 1. Location of sightings of Western Sandpipers banded in Perú, México, British Columbia, and Alaska up to 28 February 1996. Some sightings are omitted for clarity. Stars indicate banding site, squares indicate locations of sightings during winter (Oct.–Feb.), triangles are during northward migration (March–May), and circles are during southward migration (July–Sept.).

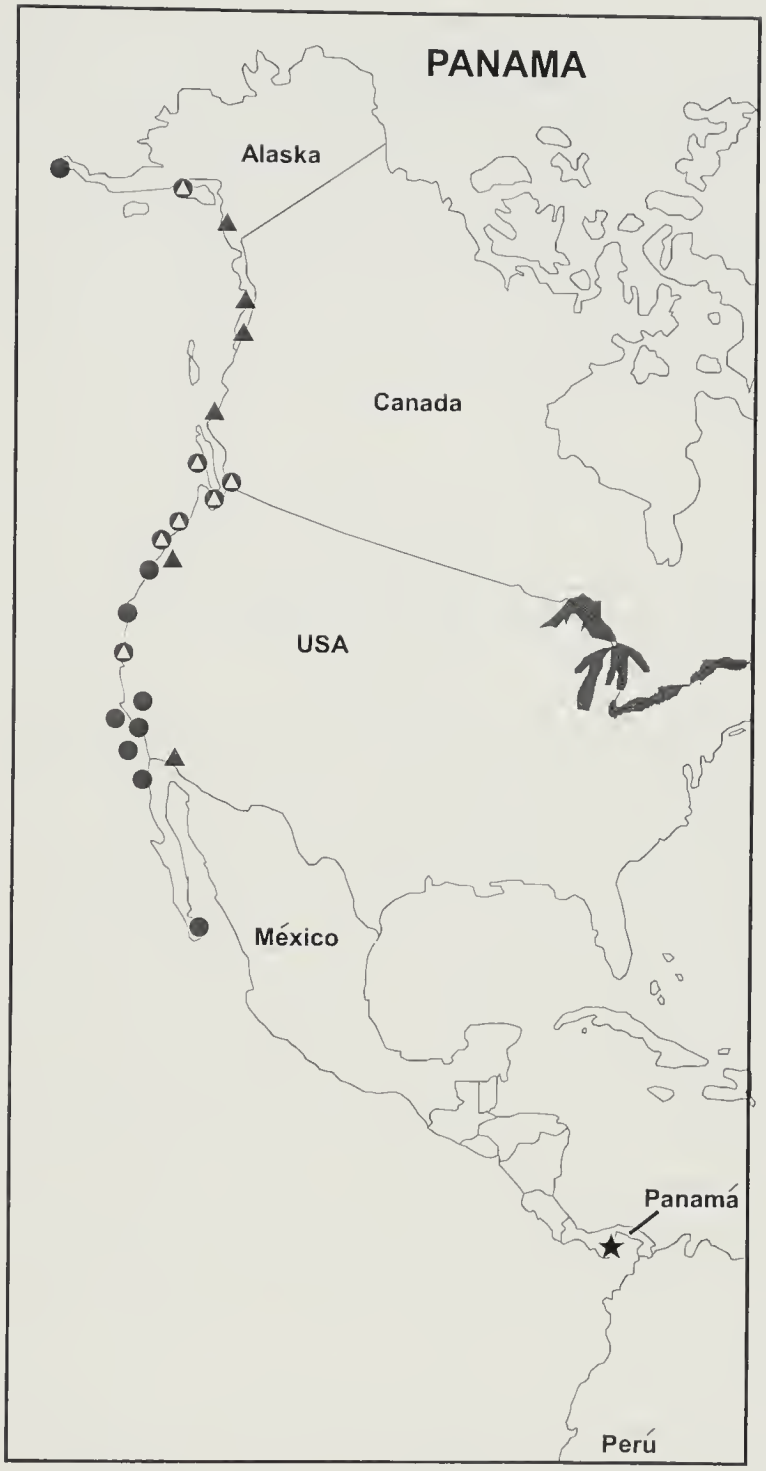

FIG. 2. Location of Western Sandpipers banded in Panamá up to 28 February 1996. Symbols as in Fig. 1.

TABLE 1

NUMBER OF SIGHTINGS AND RECOVERIES BY 28 FEBRUARY 1996 OF WESTERN SANDPIPERS BANDED AT FIVE SITES ALONG THE PACIFIC COAST

Banding site	Perú	Panamá	México	USA						BC	AK	Total
				CA	OR	WA	TX	AZ	KS			
Perú	—	0	0	1	0	0	1	0	0	1	2	5
Panamá	0	—	2	11	7	1	0	0	0	18	16	55
México	0	0	—	4	1	0	0	0	0	4	1	10
BC	0	0	0	1	0	0	0	0	1	3	1	6
Alaska	0	4	2	3	5	1	0	1	0	5	—	21
Total	0	4	4	20	13	2	1	1	1	31	20	97

bands to prevent confusion. We discarded any records when the observer was in doubt about the color of a flag or if the country of origin was in doubt.

RESULTS

Ninety-seven sightings of flag-banded Western Sandpipers were reported by 29 February 1996 (Table 1). Five sightings were from sandpipers banded in Perú, 55 from Panamá, 10 from México, six from British Columbia, and 21 from Alaska (Table 1). No flag-banded birds from the other banding sites were seen in Perú, four were seen in Panamá, four in México, 38 in continental US, 31 in British Columbia, and 20 in Alaska (Table 1). Two of the 97 sightings were made east of the Rocky Mountains; one in Kansas and one in Texas (Table 1, Fig. 1). The Kansas record was from a juvenile male Western Sandpiper banded on Sidney Island, BC on 2 August 1990 and last seen there 3 August. It was subsequently captured 2200 km to the southeast at Quivira National Wildlife Refuge, Kansas on 25 August 1990. The Texas record was of a sandpiper banded in Perú and seen near Corpus Christi, Texas on 16 December 1989. The remaining 95 sightings were made west of the Sierra Madre Mountains of México, the Rocky Mountains of the US, and the Coast Range of Canada (Figs. 1, 2).

Western Sandpipers banded in Panamá were seen on the northward and southward migrations only in Pacific Coast states and provinces of North America (Fig. 2). The migration route through the western US and Canada includes many coastal and inland sites along the west side of the Sierras and Cascade Mountains from the Gulf of California to the Strait of Georgia, British Columbia (Fig. 2). Sightings of marked birds away from the coast include Salton Sea, San Leandro and China Lake, California, and Sauvie Island and Salem, Oregon. From southern British Columbia through Alaska, sightings were confined to coastal locations.

At the close of the breeding season, Western Sandpipers gathered in flocks on mudflats near the breeding grounds at Nome where they gained about 3 g of mass prior to departure (B. Sandercock, unpubl. data). An adult female and two juvenile sandpipers of unknown gender that were equipped with radio-transmitters were detected on the Fraser River delta 28, 23 and 29 days after release, respectively. The respective average speeds of these individuals over the 4000 km distance between Nome and the Fraser River delta were 142, 173, and 137km/d, respectively. These records coupled with sightings of flag-banded birds, indicate that Western Sandpipers from at least as far north as Nome, Alaska, migrate south along the Pacific Coast.

DISCUSSION

Many species of shorebirds use different migratory routes in spring and autumn (Morrison 1984, Alerstam 1990, Gratto-Trevor 1994). Censuses of shorebirds in the western US indicate that nine sites hold over 100,000 Western Sandpipers on a single day during spring migration. They are San Francisco Bay and Humboldt Bay, California, Grays Harbor, Washington, the Fraser River delta, British Columbia, and the Stikine, Copper river deltas, Redoubt Bay, Kachemak Bay, Alaska (G. W. Page, W. D. Shuford, J. E. Kjelmyr, and L. E. Stenzel, unpubl. data). On the southward migration, flocks are much smaller at all sites and most notably in south-central and southeast Alaska, which is largely avoided by Western Sandpipers (Senner 1977; R. Gill, C. Iverson, and M. A. Bishop, pers. comm.; this study). This contrasts with sites in southern British Columbia and many western states in the US where many more sites are used in autumn than in spring migration (Paulson 1993).

The migration of the Western Sandpiper is more compressed in time and space in spring than in fall. Many of the large mudflats along the Pacific Coast of North America support larger numbers of Western Sandpipers on the northward migration than on the southward migration (Page et al. 1979; Butler 1994; Senner 1977; G. West, pers. comm.), and many small mudflats avoided in spring are used by southbound migrants. As a result, population censuses on large mudflats are greater during the northward migration than the southward migration. This phenomenon confounds our understanding of the southward migration. Gill (1979) reported two sightings of Western Sandpipers marked at Nelson Lagoon in the northern Gulf of Alaska and Prince William Sound and two sightings of birds marked on the Yukon River delta at Nelson Lagoon. He proposed that the migration route of juvenile Western Sandpipers was south along the Alaska and British Columbia coast. However, some Western Sandpipers might also make a trans-Pacific flight from western and southern

Alaska that bypasses southeast Alaska and makes landfall in southern British Columbia. Large numbers of post-breeding Western Sandpipers gather on intertidal mudflats near their breeding grounds in western Alaska and on the Alaskan Peninsula (Gill and Jorgenson 1979, Connors 1984, Gill and Handel 1990, this study). Individuals caught at this time near Nome were about 3 g heavier than their breeding masses (B. Sandercock, unpubl. data), and mass gains occurred among post-breeding Western Sandpipers on the Alaskan Peninsula (R. E. Gill, Jr., pers. comm.), suggesting they were preparing for a long flight. Banded individuals on the southward migration were seen in southern Alaska and on the Alaskan Peninsula but not southeastern Alaska (Gill 1979; Figs. 1, 2). The species occurs in very small numbers in southeast Alaska at this time (M. A. Bishop, R. E. Gill, C. Iverson, pers. comm.). Maximum single day censuses of adults and juveniles using the Fraser River delta during their southward migration were about 21,000 and 45,000 birds, respectively, which is far below the 500,000 individuals counted in spring (Butler 1994), but many other coastal and interior sites are also used mostly only during the southward migration.

Senner and Martinez (1982) proposed that most Western Sandpipers used a Pacific Coast route to and from the breeding grounds in western Alaska. Our study confirms their hypothesis for the Pacific route and extends it over 8000 km south of California to Perú (Table 1, Figs. 1, 2). Western Sandpipers banded in Perú, Panamá, and northern México were sighted along the Pacific Coast of the Americas from northern México to southwestern Alaska (Figs. 1, 2).

Evidence for the existence of a Great Plains route beginning in northern Alaska (Senner and Martinez 1982) is less convincing than the Pacific Coast route. Individuals banded near Nome and Kotzebue, Alaska have been sighted and recovered along the Pacific Coast (Fig. 1; D. Schamel, pers. comm.), but the route taken by populations that breed along the North Slope of Alaska are unknown. The species is considered as a rare breeding species in northern Alaska (Johnson and Herter 1989, Wilson 1994), and small numbers of Western Sandpipers have been seen in spring and fall migration on the northeast coast of Alaska and western Canadian arctic (Martell et al. 1984, Johnson and Herter 1989). The species is rarely seen in Alberta. Birdwatchers there recorded an individual on 20 May 1990, four individuals on 2 July 1993, and one individual on 6 May 1995 at Beaverhill Lake Bird Observatory near Edmonton between 1986 and 1995 (G. Holroyd and D. Ross, pers. comm.). None has been caught in James Bay, the Canadian Prairies, or North Dakota despite extensive banding there (D. Lank, R. I. G. Morrison, C. L. Gratto-Trevor and G. Beyersbergen, pers. comm.). This evidence suggests that the Canadian

prairies and adjacent parts of the US are north of the main migration route across the North American continent or that Western Sandpipers fly over the Great Plains on their way to and from northern Alaska.

A diagonal migration across the North American continent proposed by Senner and Martinez (1982) is the most plausible route for populations that spend the winter along the Atlantic and Caribbean coasts. This route was supported by recoveries and from sightings of banded sandpipers in this study. The most probable migration route occurs along a wide front from southern Alaska and the north Pacific Coast through continental US. The Western Sandpiper is an abundant autumn shorebird species on the south coast and in the southern interior of British Columbia, but it is uncommon farther north in the interior of the province (Campbell et al. 1990). In Idaho, the species is widespread in fall but not in spring (Oring 1962, Taylor et al. 1992), and it is abundant in mid-western US (Martinez 1979, Neil 1992, Skagen and Knopf 1993). The species is a regular winter resident on the southern Atlantic Coast of the USA and in the Caribbean (Wilson 1994, Rice 1995).

The migration routes of Western Sandpipers through Central America and northern South America are poorly known. Hundreds of thousands of Western Sandpipers spend the winter on the Pacific coasts of México (Morrison et al. 1992, 1994) and Panamá (Butler et al. 1992b). We assume that the migration route south of México follows the Pacific Coast but records are lacking. The sighting of a Peruvian banded bird in Texas in December is enigmatic, given that the species exhibits strong winter site fidelity (Smith and Stiles 1979, Rice 1995).

Evidence to support Wilson's (1994) contention that migration is more leisurely in fall than in spring is equivocal. Fifty-eight adult spring migrants carrying 0.8 g mass radio transmitters flew the 3200 km distance between San Francisco Bay and Copper River delta at an average speed of 422 km/d (Iverson et al. 1996). This is 1.3–3.0 times faster than the speed we found for autumn migrants flying 4000 km between Nome and the Fraser River delta. However, some of this time might have been spent accumulating mass in preparation for migration. Once migration was underway, individuals appeared to travel at similar speeds: the length of stay at Pacific Coast staging sites is about three days in spring and autumn (Butler et al. 1987, Iverson et al. 1996).

The trans-Pacific flight of the Western Sandpiper likely evolved during the last glacial period about 15,000 BP. During the height of glaciation, sea level along the Pacific Coast was about 100 m lower than today. Much of the present day continental shelf off Washington, Oregon, and California was not covered by water. In Alaska, Beringia extended over 1000 km wide in places, providing tundra habitats for many shorebirds. Be-

tween the breeding grounds in Beringia and the beaches of continental US lay an immense sheet of ice requiring flights of about 3000 km by shorebirds migrating to winter quarters in Central and South America. The river deltas in British Columbia and Alaska are less than 9000 years old, and so their use by Western Sandpipers is a relatively recent phenomenon. It is unclear why shorebirds use these deltas in spring but not fall but the answer may lie in the nature of favorable winds for migration. In spring, winds along the British Columbia and Alaska coasts are frequently from the southeast and in the direction of the migration, whereas late summer winds are generally out of the northwest (Favorite et al. 1976). We hypothesize that Western Sandpipers migrate northward along the coast and southward across the Pacific to take advantage of favorable winds.

ACKNOWLEDGMENTS

Many people assisted us while banding sandpipers, including S. Cullen, S. Gonzalez, L. Imbeau, N. Imbeault, G. Kaiser, M. Lemon, P. O'Hara, K. O'Reilly, Y. Sandoval, C. Schmidt, C. Schuppli, P. Shepherd, C. St. Pierre, T. Sullivan, N. Warnock, and S. Wyshynski. We also thank the many people who sent us their sightings of flag-banded birds and observations, including C. Gratto-Trevor, G. Holroyd, J. Lyons, D. Ross, N. Tsipora, and staff at Manomet and Point Reyes bird observatories. Gary Page generously allowed us to use shorebird census data of California, Oregon, and Washington between 1988 and 1992 belonging to Point Reyes Bird Observatory. Bob Gill and Doug Schamel shared their knowledge of the species in Alaska. Our field studies in Nome and Sidney Island, British Columbia, were permitted by the Sitnasauk Native Corporation and BC Ministry of Parks, respectively. The manuscript was improved by comments from R. E: Gill, C. Hitchcock, D. Lank, G. Morrison, N. Warnock, and an anonymous referee. This project was funded by the Canadian Wildlife Service (CWS), CWS Latin American Program, CWS/NSERC Chair in Wildlife Ecology at Simon Fraser Univ. (SFU), graduate fellowships from Queens' Univ. and SFU, Northern Studies Training Program, Frank M. Chapman, John K. Cooper, and Jennifer Robinson memorial awards, and Centro de Investigacion Cientifica y de Educacion Superior de Ensenada.

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Wilson Bull., 108(4), 1996, pp. 673–684

BREEDING BEHAVIOR AND REPRODUCTIVE SUCCESS OF CERULEAN WARBLERS IN SOUTHEASTERN ONTARIO

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ABSTRACT.—Little is known about the breeding biology of the Cerulean Warbler (*Dendroica cerulea*), a species declining throughout much of its range. However, life history information can provide important insight into the vulnerability of a rare species to habitat disturbance. We studied the breeding behavior of Cerulean Warblers at three different sites in southeastern Ontario through the breeding season, from early May to late July 1995, and at one of the above sites in 1994. Twenty-seven nests, including three renests, were located within 27 territories. Average territory size was 1.04 ha (N = 18). Although both males and females displayed at potential nest sites, building was performed only by females and took five to six days. Nest trees were predominantly sugar maple (*Acer saccharum*) or oak (*Quercus spp.*), with an average height of 17.7 m and an average diameter at breast height (DBH) of 40.2 cm. Average nest height was 11.8 m. There were no incidents of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) and nest loss due to predation was low (14%). Incubation, performed only by females, lasted 11 to 12 days. Clutch size ranged from two to five eggs, with a modal clutch size of 5 (N = 6). During the 10 to 11 day nestling period, both males and females fed the chicks equally. Reproductive success in this population was high in both years. Twenty of the 27 pairs successfully fledged young, with a mean of 3.2 fledglings per successful nest. Record increases, and the high reproductive success of Cerulean Warblers in the Frontenac Axis area of the Canadian Shield, may be the result of reforestation of agricultural lands abandoned at the turn of the century. *Received 28 Nov. 1995, accepted 15 April 1996.*

The Cerulean Warbler (*Dendroica cerulea*), like many other Neotropical migrants, is a species of conservation concern. Robbins et al. (1992) found that between 1966 and 1988, Cerulean Warblers declined at an average rate of 3.4% per year, the greatest decline for any species of warbler during that period. Currently listed as vulnerable in Canada (McCracken 1992), its dependence on large tracts of mature deciduous forest for successful breeding may make the Cerulean Warbler especially sensitive to continuing forest fragmentation and isolation (Adams and Barrett 1976, Temple 1986, Robbins et al. 1992, Parker 1994). Concurrent with this overall decline, several authors have suggested that Cerulean Warblers are undergoing a northeastern expansion of their range as agricultural lands abandoned at the turn of the century are allowed to succeed to mature forest (Ouellet 1967, Laughlin and Kibbe 1985, Andrle and Carroll 1988, Hamel 1992, Maurer 1994). This may be the case in Ontario.

The northernmost portion of the Cerulean Warbler's range occurs in

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the mixed deciduous forests from the Bruce Peninsula to eastern Ontario, Canada, with a concentration on the Frontenac axis, at the northeast tip of Lake Ontario (Cadman et al. 1987). Local records suggest a gradual increase in the number of Cerulean Warblers in the Kingston area. Since sporadic sightings began in the 1930s, the birds have been found annually since 1961 (Weir 1989).

While interest in the Cerulean Warbler appears to be growing, details of its life history, necessary for establishing management and conservation programs, are incomplete. In this paper, we provide descriptions of the breeding behavior, nesting chronology, habitat use, and breeding success of a population of Cerulean Warblers in southeastern Ontario.

METHODS

During the spring and summer of 1995, we monitored a population of Cerulean Warblers at three 9-ha study sites near the Queen's Univ. Biological Station (QUBS), Lake Opinicon, Leeds/Frontenac Counties, Ontario, Canada (44°30′N; 76°23′W). The sites were selected as areas where Cerulean Warblers had been recorded with greatest regularity and highest density based on breeding bird surveys (R. Weir, pers. comm.). In 1994, a less intensive, preliminary study was conducted at one of the sites. Nests located in 1994 are included in the results on nesting success and nest-tree species use; all other results are based on data collected in 1995 alone.

The physiography of the region around QUBS consists of shallow till soils with rock ridges and undulating topography (Chapman and Putnam 1984). The area was initially cleared for agriculture in the early 1800s, but the amount of forest cover has increased since the early settlement period, as a result of abandonment of farmland and reduction of timber harvesting (Keddy 1994). The forest at all three sites is now characterised by second-growth mixed deciduous forest, dominated by sugar maple, with components of ironwood, oak, elm, ash, hickory, basswood, and birch (see Table 1 for scientific names of trees).

All three sites were contained within a region of extensive forest cover interspersed with lakes, roads, and some small agricultural fields—an area which is more or less contiguous with extensive forests on the Canadian Shield to the north without significant interruptions of agriculture or urban development. Consequently, limits of forest patch size were not easily determinable either from topographic maps or aerial photos, and any attempt to define forest area would be arbitrary at best. Two of the sites were located about 500 m apart, while the third site was separated from the other two by approximately 15 km of forest and open water (Fig. 1). Because of small sample sizes, observations from all three sites were pooled for analyses.

To determine territory size, territorial boundaries were mapped in early May using playback (Falls 1981). We used a Sony Professional Walkman in combination with a single Sony SRS-77G, 25 watt speaker (audible to a distance of about 100 m) to broadcast the song of an unfamiliar conspecific to a territorial male. This method stimulates territorial males to sing, and draws them out to the boundaries of their territory. A boundary point is established either when the bird no longer approaches or a neighbor approaches the playback speaker. Each of the study plots consisted of a 6.25-ha grid marked with flagging tape every 25 m and represented only a sample of the total population in the area. Territories with boundaries at least 50% within a 6.25-ha grid were drawn on a map (Fig. 1). Territorial disputes, involving bouts of countersinging or fighting, were also mapped and used to con-

TABLE 1

CHARACTERISTICS OF NEST PLACEMENT FOR CERULEAN WARBLERS

Tree species	N	Tree height (m)	Nest height (m)	DBH (cm)	Dist. from trunk (m)	Dist. from canopy gap (m)
Sugar maple (*Acer saccharum*)	18	18.5 ± 0.64[a]	11.9 ± 0.53	44.6 ± 5.2	4.3 ± 0.39	35.8 ± 6.2
Burr oak (*Quercus macrocarpa*)	3	12.8 ± 1.6	9.1 ± 0.46	39.1 ± 15.8	2.6 ± 0.41	24.3 ± 13.1
White oak (*Q. alba*)	2	19.9 ± 1.9	14.7 ± 2.2	30.3 ± 0.25	2.0 ± 2.0	19.3 ± 6.4
Red oak (*Q. rubra*)	1	19.6	18.6	24.0	2.0	26.9
Ironwood (*Ostrya virginiana*)	1	9.5	7.0	11.2	1.8	79.0
Bitternut hickory (*Carya cordiformis*)	1	20.0	8.0	38.7	2.5	12.0
American elm (*Ulmus americana*)	1	16.0	14.0	32.9	3.0	29.7
Overall mean	27	17.7 ± 0.67	11.8 ± 0.56	40.2 ± 5.1	3.62 ± 0.33	33.4 ± 4.7

[a] Mean ± SE.

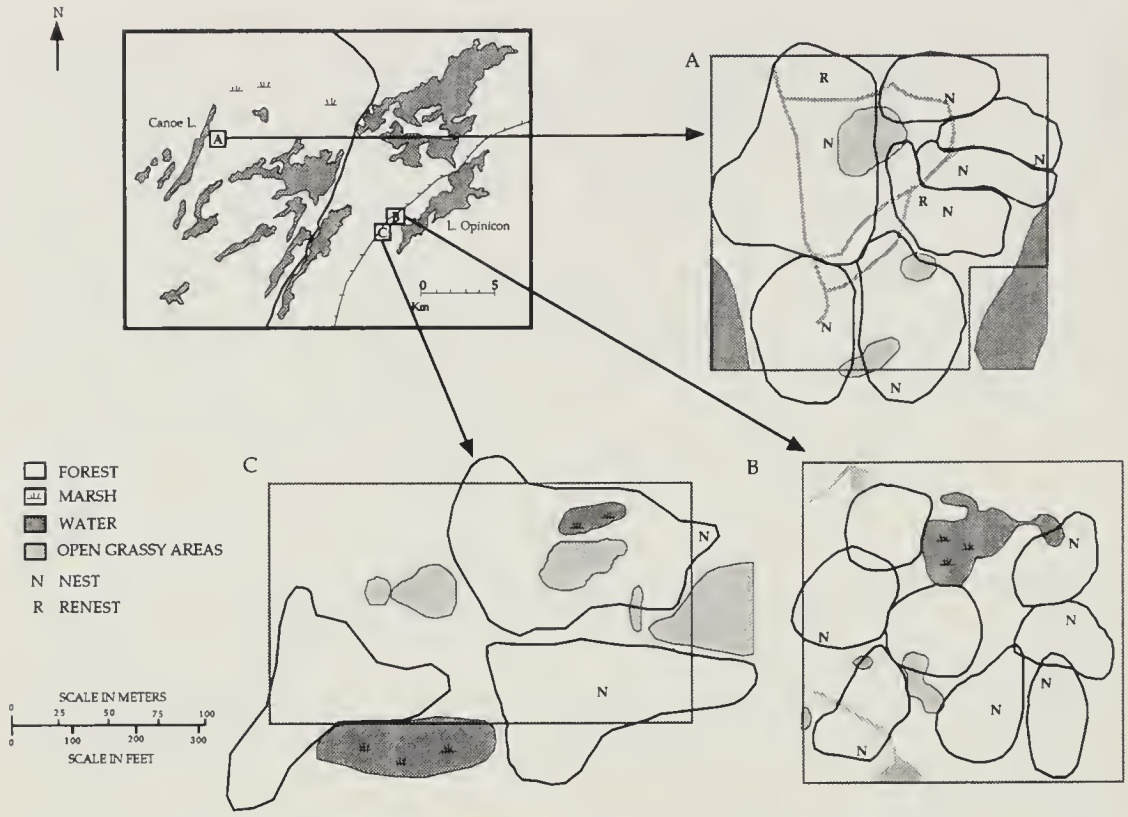

FIG. 1. Map of 18 Cerulean Warbler territories in 1995 at three sites (A = Hahn, B = Bedford Mills, and C = Lindsay Lake) near Lake Opinicon, Ontario (site A was studied in both 1994 and 1995). Outline shows the boundary of each 6.25-ha study site.

firm borders between neighboring males. To increase confidence in the boundaries, five males were banded with a Canadian Wildlife Service metal band and two color bands in early June (at least one per site). Males were captured using aerial mist nets raised to a level of approximately 10 m, accompanied by playback and model presentation. All subsequent observations of these males occurred within the previously recorded boundaries.

Territories were visited at least twice a week for periods of 30 to 60 minutes to search for nests for the duration of the breeding period, or until the nest was located. If a nest failed, the territory was monitored for renesting. Nests were monitored every second day to determine the length of the nest building, incubation, and nestling periods. Incubation period was considered to be the time between the first prolonged visit to the nest by the female ($\geq$20 min) and the first observed feeding visit. Behavior at the nest, such as feeding rates and duration of parental visits, was recorded during 60-min nest watches between 07:00 and 08:00 EST on days 3, 7, 10, 14, 17, and 20 of the nesting cycle. On the estimated day of fledging, nests were monitored starting at 05:00 EST in order to count the number of chicks leaving the nest. For nests that were not clearly observable from the ground, in addition to monitoring the nest on the day of fledging, the nest tree was climbed on day 7 or 8 of the nestling period to give a maximum estimate of the number of young likely to fledge. In 1994, six trees were climbed during the incubation period, and this information was used to determine clutch size. Trees were climbed using ropes, a leather climbing belt, and occasionally, climbing spurs. Once the observer was at nest height, nest contents were examined using an extendible mirror pole to determine brood size and degree of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*).

Parasitism by Brown-headed Cowbirds has been implicated in reducing reproductive success in certain forest songbirds (Brittingham and Temple 1983), including Cerulean Warblers in northwestern Ohio (Mayfield 1977). To determine the density of cowbirds in the area of the study sites, we recorded each visual or acoustic identification of Brown-headed Cowbirds throughout the breeding season.

We recorded nest-tree species and measured five characteristics at each nest: tree height, nest height, diameter at breast height (DBH), distance of nest from the trunk, and distance of nest tree to the nearest canopy gap. We defined a canopy gap as an area where the height of the vegetation changed abruptly from average canopy height to ground level, such as a dirt road, rock outcrop, field, or open water. Heights were measured using a rangefinder and DBH was measured using a diameter tape.

RESULTS

Territorial behavior and pair formation.—Males began to arrive in the area during the first week of May. Before pairing, males moved around their territories singing from high, often exposed, perches. The male song has been described as *zray, zray, zray, zree* with the final *zree* syllable sliding upwards slightly in pitch (Peterson 1980). Variations of this song occurred between individuals (R. Woodward, unpubl. data). Females did not sing, but both males and females used a soft, high-pitched, metallic "chip" note which is used as a contact and alarm call. The chip note of the male was shown on a sonagram to be slightly lower in frequency than that of the female, but the difference is difficult to distinguish by ear (C. Oliarnyk, unpubl. data).

Territories ranged from 0.38 ha to 2.4 ha, with a mean size (±SE) of 1.04 ± 0.16 ha (N = 18). Territories covered most of the area of the study grids, and boundaries of several territories abutted one another (Fig. 1). Males defended territories with bouts of counter-singing with neighboring males at the boundaries of their territory. Eight times, physical disputes were observed between males, in which one male would either supplant another from a perch (N = 6) or make contact in mid-air (N = 2).

Females arrived the second week of May, and pairs spent the first couple of days foraging close together. During this courtship period, several pairs were observed in short chase flights initiated by the male. Females were also sometimes involved in disputes between neighboring pairs (N = 5).

Nest construction.—Nest-site selection and construction began one to two days after the arrival of the female on a territory. Both males and females were seen displaying at potential nest sites by spreading their wings and fanning their tails in combination with nest-shaping motions. This behavior was usually performed with the mate nearby, and often the observing mate would replace the displaying individual and repeat the

display (N = 5). Only two copulations were observed, one at a nest, the other about 75 m from a nest.

Once a nest site was selected, interactions between males and females were infrequent. Usually they were seen together less than once every half hour. Nest building was performed entirely by the female, and lasted 5–6 days, not including the egg-laying period. The range of dates for initiation of construction for known first brood nests was 18 May to 24 May (N = 12) and for renests was 31 May to 4 June (N = 3).

Nests were open, shallow cups resembling a knot on a branch when viewed from the ground. The exteriors were formed from bark strips, grasses, and other plant fibres. Linings were made of spider webs, fine bark strips and soft plant material. Lichen and birch bark "shingles" usually covered parts of the exterior of the nest. Five nests were collected and measured and had the following dimensions (mean ± SE): outside diameter 6.5 ± 1.2 cm, inside diameter 5.0 ± 0.6 cm, outside depth 3.3 ± 0.7 cm, and inside depth 3.0 ± 0.9 cm.

Nest location.—In 1995, 17 nests, including two renests, were located in 15 of the 18 mapped territories. Adults were observed feeding fledglings in two of the three territories where nest sites were not determined. Therefore, we assume that nesting efforts were made in most, if not all, of the 18 territories. One female abandoned her first nest during the early part of the incubation period, possibly due to the presence of an Eastern Wood-Pewee (*Contopus virens*) nest 1.7 m from it in the same tree. In 1994, ten nests were located, one of which was a renest. In all three instances of renesting, the second nest was constructed using material from the previous nest which was carried to the new site. No second broods were found in either 1994 or 1995.

Seventy percent of nests were located within ten meters of a territorial boundary, and over half (59%) were within thirty meters (mean distance ± SE = 33.4 ± 4.7 m, N = 27) of a canopy gap (see Fig. 1). In a random sample of points taken from within a territory, only 23% were within 30 m of a gap. It should be noted that in only one case did a nest occur near a gap between differing, adjacent habitat types. Most were contained within patches of otherwise continuous forest. The majority of nests were found in the lower third of the canopy (71%), had no other vegetation between the nest and ground cover (understory gap) (59%), and were found on the outer edge of a lateral branch (77%). The most commonly used tree species for nesting were those with the greatest overall basal area; sugar maple (N = 18) and oak spp. (N = 6) (Table 1). Sugar maple was the dominant species in all three sites, and oaks were the second most abundant species group with mean total basal areas of 199.58 $m^2 \cdot ha^{-1}$ and 128.71 $m^2 \cdot ha^{-1}$ respectively.

Clutch size.—Clutch size ranged from two to five eggs (mean ± SE = 3.8 ± 0.22, N = 6), with five being the modal clutch size. We found no Brown-headed Cowbird eggs in any of the six nests examined before hatching, and no cowbird chicks being fed either during the nestling period or after fledging. Cowbirds were recorded only two or three times at each of the three sites and only during the period between 12 May and 12 June.

Incubation.—Incubation was performed by the female and lasted between 11 (N = 5) and 12 (N = 3) days. The first incubating female was found on 30 May, and the last day of observed incubation was 23 June. The mean (±SE) total incubation time per hour was 50 ± 5.3 min (N = 18 h, 9 nests). Males were twice observed feeding females on the nest during incubation (N = 20 h, 9 nests). Contact was maintained by call notes from incubating females in response to their mate's song. Females also sometimes gave call notes when they left the nest.

Nestlings.—The nestling period lasted between 10 (N = 6) and 11 (N = 4) days. Female attentiveness remained high for the first one to three days after hatching, with the female spending a mean (±SE) of 49.2 ± 4.7 (N = 5 h, 5 nests) min per hour brooding the nestlings. Time spent at the nest by the female declined progressively as the nestlings matured (Fig. 2), with females spending less time brooding the nestlings and more time standing near, or on, the edge of the nest. Males spent minimal time at the nest, usually just long enough to feed the young. Both males and females fed the young as soon as they hatched, with males and females feeding approximately equally (mean feedings/h ± SE; males = 3.5 ± 1.8, females = 3.5 ± 3.7, N = 17 h, 8 nests).

On the day of fledging, activity and noise from the parents and chicks were high, with both the male and female chipping rapidly and continuously, and the chicks begging for food. Several pairs also showed alarm at our presence for the first time on fledging day. This activity made locating already fledged chicks relatively easy, however, direct observation of the chicks after the day of fledging was difficult. Fledglings used all parts of the canopy, were often hidden under leaves, and their call was very difficult to isolate. In addition, chicks responded quickly to parental alarm calls. On two occasions, when a male gave a chip note, nestlings ceased all begging calls and movement and did not resume until the male began to sing again. In begging behavior the fledgling crouched down low on the branch, fluttered its wings, and gave high-pitched, burry call notes. All young had fledged by 4 July. One pair was observed feeding young 19 days after fledging. Adults were observed feeding chicks within territorial boundaries at least 10 days after fledging in 50% of the successful territories. If parents were observed feeding fledged young within

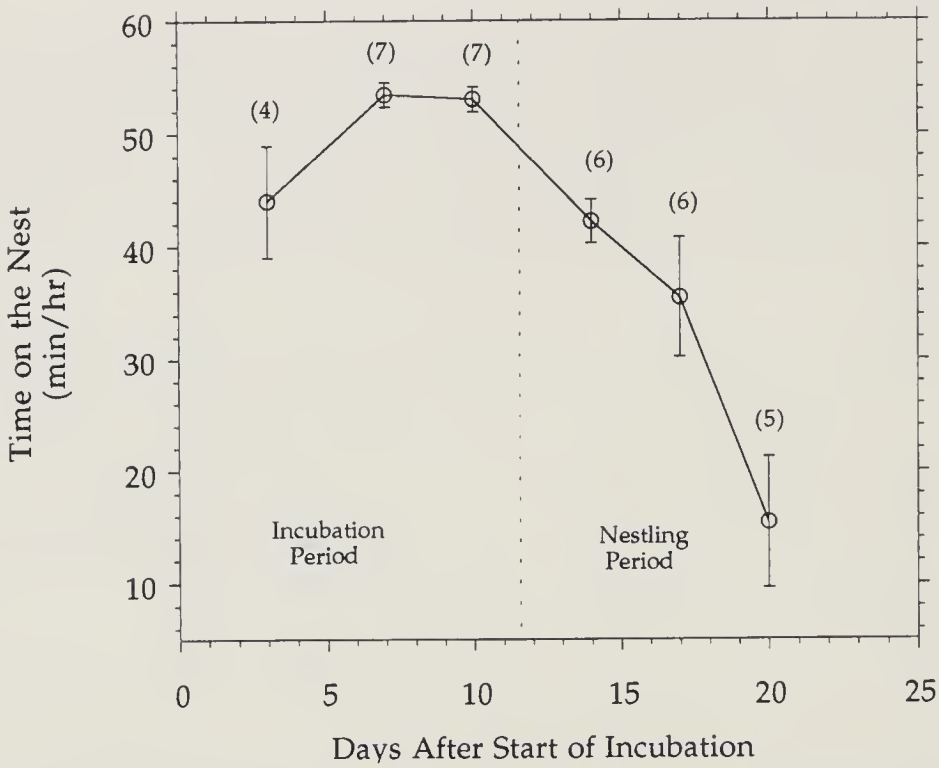

FIG. 2. Time (mean ± SE) spent at the nest by female Cerulean Warblers during the nesting cycle, based on 35 one-hour watches at nine different nests. Time 0 is the start of incubation and vertical dotted line indicates the start of the nestling period. Sample size is indicated in brackets above each point.

the bounds of a territory, they were assumed to belong to the territorial pair; however, family groups are likely quite vagile. For example, one banded male was observed feeding a fledgling approximately 100 m from the edge of his territory, within the territory of an unpaired male.

Nesting success.—Twenty of 27 pairs successfully fledged young over the two years of the study. No significant difference in reproductive success (successful fledging of at least one chick) existed between years (Fisher Exact Test, $P = 0.65$, df = 1). The mean (±SE) number of young in nests examined before fledging was 3.6 ± 0.2 (N = 8). This is slightly higher than the number based on observations of fledging from the ground 3.2 ± 0.2 (N = 20).

Nine nests failed (five in 1995, four in 1994). Four nests were likely depredated. Two of these nests failed during the nestling stage and although no evidence of nestlings was found, almost the entire bottom of both nests was torn out, suggesting predation. The other two nests failed early in the incubation stage. In all cases of suspected predation the female was probably preyed on as well. No subsequent observations of females were recorded on these territories from the time of nest failure to the end of the breeding season in mid-July. Males on these territories

also resumed behavior characteristic of unpaired males, such as continuous singing from high, exposed perches for extended periods of time. It is not known what preyed on these nestlings and females, but Blue Jays (*Cyanocitta cristata*) and Red-shouldered hawks (*Buteo lineatus*) were sometimes heard in the area. Gray squirrels (*Sciurius carolinensis*) were observed in trees containing nests—at nest height. On one occasion a black rat snake (*Elaphe obsoleta*) was observed in a nest tree above nest height, approximately one hour after the nestlings had fledged.

The reason for the abandonment of the other five failed nests is unknown although, as mentioned earlier, interspecific interference may have played a role. Females from three of these territories renested, but the status of the other two was not determined.

DISCUSSION

Despite increasing data demonstrating declining trends in Cerulean Warbler numbers, this local population appears to be relatively successful. Low instances of nest predation and brood parasitism suggest that, in this area at least, Cerulean Warbler numbers are not limited by poor reproductive success.

Based on results from our study plots, Cerulean Warbler density in this area may be as high as 96 prs·km^{-2}, assuming uniform conditions. Across Ontario, Cerulean Warblers were recorded in only 6% of the 10 × 10 km breeding bird atlas squares (Cadman et al. 1987). In areas where Ceruleans did occur, 80% of abundance estimates are of fewer than 11 pairs per atlas square. Based on these results, the density of birds around Kingston appears to be much higher than in the rest of Ontario. This may be related to the higher proportion of forested land in the area around Kingston relative to the more southerly parts of Ontario. However, it should be noted that an inconspicuous, forest interior bird such as the Cerulean Warbler may occur over a greater range or at a higher density than is indicated by breeding bird surveys (Cadman et al. 1987, Terborgh 1989). The density of birds, and consequently territory size, differed between the three sites; 1.12 prs·ha^{-1}, 1.28 prs·ha^{-1}, and 0.48 prs·ha^{-1} at sites A, B, and C respectively. Hamel (unpubl. data) has suggested that Cerulean Warblers seem to breed in loose "colonies". Since all three sites are the same forest type, the difference in density between the adjacent sites, B and C, may reflect this colonial nature, with site C acting as a spillover area for the more saturated site B.

The mean nest height of 11.8 m falls within the 5 to 18 m range of nest heights cited in the literature (Saunders 1900, Harrison 1984). Maple, oak, and elm were the three most commonly cited species of nest tree across the range of the Cerulean Warbler (Saunders 1900, Bent 1963 and

references therein, Ouellet 1967, Bull 1976, Laughlin and Kibbe 1985, Peck and James 1987, Andrle and Caroll 1988). In this study, nests were most often located in sugar maple and oak spp., the dominant tree species at all three sites. Since insufficient information is provided on dominant tree species in the literature, it is not possible to determine whether Ceruleans use trees in proportion to occurrence, throughout their range.

The high proportion of nests associated with understory and canopy gaps, has also been noted by other authors (Bent 1963, Harrison 1984, Peck and James 1987). These apparent associations with gaps may be an important component of Cerulean Warbler nest-site selection. Examination of Fig. 1, and a comparison of nest location versus random locations within a territory, suggests that nests may be associated with gaps such as water, paths, or open areas in greater proportion than their availability within the territory. It is unlikely that this result is due to observer bias in locating easily observable nests associated with gaps, since nests were located in 83% of the territories. However, detailed analyses of habitat data are necessary before any definitive conclusions can be made about the role of gaps in nest-site selection.

The mean clutch size of four is the same as the mean clutch size of nests located in southern Ontario (N = 36) (Peck and James 1987). The modal clutch size of five, however, is a new record for Ontario (Peck and James 1987). In 35 nests in New York state, the average clutch size was again four eggs (51%), with nests also containing three eggs (26%) and five eggs (23%) (Bull 1976). The lack of brood parasitism by Brown-headed Cowbirds was noteworthy for the Ontario range. In southwestern Ontario, the incidence of Brown-headed Cowbird parasitism of Cerulean Warbler nests is as high as 17.9% (Peck and James 1987).

The incubation period of 11 to 12 days determined in this study is similar to Harrison's (1975) speculation that the incubation period is 12 to 13 days.

Cerulean Warbler habitat has been described as mature, riparian forest (Bull 1976, Lynch 1981, Laughlin and Kibbe 1985). The area of maturing second-growth forest, dotted with numerous lakes and streams, north of Kingston approaches this description. Forests in this area are also compositionally similar to forests present before extensive post-settlement alteration (Keddy 1994); therefore, the recorded northeastern expansion of the species may be a reoccupation of habitat within the species range prior to European settlement. Unfortunately, no records of Cerulean Warblers in this area exist prior to 1930 to confirm this theory.

The establishment and success of this northern population of Cerulean Warblers over the past two decades is likely the result of reforestation of areas rendered unsuitable by European colonization in the northern range

of the Cerulean Warbler. With forested areas continuing to be cleared and maintained for agriculture, and local populations being eliminated in the southern portion of its breeding range, maturing second-growth forest in the north may provide an important source area for Cerulean Warbler populations in the future.

ACKNOWLEDGMENTS

We give special thanks to Clive Goodinson, Brent Gurd, Andre Patry, and Becky Whittham for their assistance with field work; Brent Gurd, Kelvin Conrad, Paul B. Hamel, Bart Kempenaers, Wally Rendell, and an anonymous reviewer for helpful suggestions on an earlier version of this manuscript. This study was funded by a grant from the Eastern Ontario Model Forest Program and a Natural Science and Engineering Research Council operating grant to R. J. Robertson. Logistical support was provided by the Queen's Univ. Biological Station.

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Wilson Bull., 108(4), 1996, pp. 685–696

GRIT-USE PATTERNS IN NORTH AMERICAN BIRDS: THE INFLUENCE OF DIET, BODY SIZE, AND GENDER

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ABSTRACT.—We investigated avian grit use by examining the gizzard contents of 1440 birds collected from 12 states. Grit was present in gizzards of 62 of 90 species and varied greatly in number and mean particle size. Gizzards of granivorous birds contained more grit particles than those of insectivores, omnivores, and frugivores. Grit particle characteristics (mean size, shape, and surface texture) did not differ among birds consuming different diets. Mean grit size increased linearly with the common logarithm of the bird body mass. Within avian species, grit-use patterns did not differ by gender. Grit use is widespread among birds, and diet strongly influences the amount of grit used by birds. *Received 18 Oct. 1995, accepted 10 March 1996.*

Best and Gionfriddo (1991) characterized grit use by 22 species of North American birds. The impetus for that work was the relevance of grit use to avian mortality caused by ingestion of granular pesticides used to control corn rootworms and other agricultural pests (Best and Fischer 1992). Birds included in that study were limited to species that commonly use midwestern cornfields during the breeding season, when pesticides usually are applied. The present research examined grit use by a larger number of avian species, over a wider geographical area, and included many birds collected during the nonbreeding season. Our objectives were to survey grit use by a broad range of avian species and to examine the influence of diet, body size, and gender on the amounts and characteristics of grit used by birds.

METHODS

We obtained birds opportunistically from a variety of sources including road kills, collisions with windows and other objects, hunter harvests, and research projects. Birds were collected year-round and from 12 (mostly midwestern) states. We removed the gizzards from all collected birds and preserved them in ethanol. Later, each gizzard was sliced in half and its contents were flushed into a petri dish and examined under a stereomicroscope. We separated all grit particles from the other gizzard contents and excluded particles <0.1 mm in size because (1) the size distributions of grit in the gizzards of most species showed that as grit size decreased toward 0.1 mm, the number of particles per size class declined abruptly (Best and Gionfriddo 1991), and (2) we felt that particles <0.1 mm probably represented soil ingested incidentally during foraging. We then systematically counted the grit and characterized particles on the basis of size, shape, and surface texture. The longest and shortest dimensions of each particle in the 1440 gizzards we examined were measured to the nearest

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0.1 mm with a digital caliper or an ocular micrometer in the microscope. We used the average of these two values as a measure of particle size and their ratio as a shape index value. Shape index values were ≥1.0, with 1.0 representing a somewhat spherical shape and larger values representing more oblong shapes. We characterized the surface texture of each grit particle in 499 of the gizzards by using a classification system developed by petrologists to describe mineral grains (fig. 1 in Best and Gionfriddo 1991). The five surface-texture categories were angular, sub-angular, sub-rounded, rounded, and well-rounded. An overall mean surface-texture value was calculated for each bird by assigning particles in the angular category a value of 1, those in the sub-angular category a value of 2, etc.

For comparisons of grit use based on diet, we classified each bird as an insectivore, granivore, omnivore, frugivore, or carnivore, taking into account the month in which the bird was collected and following the classification of DeGraaf et al. (1985). We classified Ring-necked Pheasants (scientific names of avian species are in Table 1) collected during the non-breeding season, however, as granivores (rather than herbivores, as suggested by DeGraaf et al. [1985]) because most of their non-breeding season diet consists of seeds (e.g., Dalke 1937, Ferrel et al. 1949, Korschgen 1964). Carnivores and frugivores were excluded from some analyses because of small sample sizes.

Except for the diet-based comparisons (in which data from species with similar diets were combined), our analyses of grit use were limited to those species for which the contents of at least five gizzards were examined. This limitation was imposed because of the great intraspecific variation in the number of grit particles per gizzard, a variable for which there is only one value per gizzard. For other variables, such as grit size, shape, or surface texture, each gizzard yielded as many values per variable as there were grit particles in the gizzard.

Bird body masses were obtained from Dunning (1993). For dimorphic species used in intraspecific comparisons by gender (i.e., species with ≥5 birds of each gender included in the sample), we assigned the gender-specific masses given by Dunning (1993). For the other dimorphic species, we assigned to each bird the mean of Dunning's values for males and females.

Analysis of variance (ANOVA) was used to identify differences in grit use among birds consuming different types of foods. When ANOVA detected differences among dietary groups, we used Student-Newman-Keuls (SNK) multiple comparison tests to identify specifically which groups differed. Using data only from those species for which we examined the contents of ≥5 gizzards, we calculated Pearson product-moment correlations to examine if the mean number of grit particles per gizzard was related to grit occurrence (the percentage of gizzards containing grit) or mean grit size. We used regression analysis to examine the relationship between mean grit size and bird body size. Two-tailed *t*-tests were used to examine if mean grit counts, sizes, shape index values, or surface-texture values differed by gender. Unless otherwise indicated, a significance level of $P \leq 0.05$ was used for statistical tests.

RESULTS

Gizzard contents of birds representing 90 species and 10 orders were examined. Grit was present in gizzards of 62 species (9 orders). Frequencies of occurrence of grit in gizzards and grit counts per gizzard varied greatly among species. Species with low frequencies of occurrence of grit (and low grit counts) generally were insectivores, whereas those with high frequencies of occurrence (and high grit counts) usually were granivores. Among the 35 avian species for which ≥five gizzards were

examined, frequencies of grit occurrence in gizzards ranged from 0 to 100%, and mean grit counts per gizzard ranged from 0 to 281 (Table 1). Gizzards of Ring-necked Pheasants, American Tree Sparrows, and House Sparrows had the highest frequencies of occurrence of grit and also generally had the highest grit counts. Low frequencies of occurrence and grit counts were recorded for Eastern Kingbirds, Cedar Waxwings, Barn Swallows, Dickcissels, Common Yellowthroats, Yellow-rumped Warblers, and Northern Orioles. Grit occurrence and mean grit counts were correlated ($r = 0.502$). Intraspecific variation in grit counts was substantial: standard deviations typically exceeded mean values (Table 1).

Mean grit counts per gizzard differed among birds consuming different foods ($F_{3,1432} = 59.01$, $P < 0.001$). Gizzards of granivores contained more grit particles than those of insectivores, omnivores, and frugivores (SNK test, $P \leq 0.05$) (carnivores were excluded because of small sample size). The adjusted mean grit size (see below), mean shape index value, and mean surface-texture value did not differ among granivores, insectivores, and omnivores (size: $F_{2,969} = 2.41$, $P = 0.090$; shape: $F_{2,969} = 0.691$, $P = 0.501$; surface texture: $F_{2,490} = 2.455$, $P = 0.087$). Carnivores and frugivores were excluded because of small sample sizes.

Regression analysis indicated that mean grit size was related to bird body size, increasing linearly with the $\log_{(10)}$ of the body mass (Fig. 1). To permit examination of the relationships between mean grit size and other variables (with the effects of bird body size partitioned out), we adjusted the mean grit size for each species by adding the species' residual value to the overall mean grit size of the sample (Steel and Torrie 1980: 251). For most (22) of the 33 grit-using species for which we examined ≥five gizzards, there was no detectable relationship between the adjusted mean grit size and the number of grit particles per gizzard. In 11 species, however, a significant ($P \leq 0.01$) negative correlation was found between these variables.

Among the 17 species for which we examined ≥5 gizzards for each gender (Table 1), mean grit counts differed ($P \leq 0.05$) intraspecifically by gender only in Ring-necked Pheasants ($t = 3.40$, 31 df, $P = 0.002$) and Red-headed Woodpeckers ($t = 2.45$, 16 df, $P = 0.026$). In both species, gizzards of females contained more grit than those of males. Gender comparisons of adjusted mean grit sizes, mean shape index values, and mean surface-texture values detected few differences. Because surface-texture values were calculated only for 499 birds, sample sizes permitted gender comparisons within only five species: Northern Bobwhite, Brown-headed Cowbird, Red-winged Blackbird, Vesper Sparrow, and House Sparrow. In Brown-headed Cowbirds, females used larger ($t = 2.97$, 87 df, $P = 0.004$), less oblong ($t = 2.72$, 87 df, $P = 0.008$), and

TABLE 1
GRIT USE BY WILD BIRDS[a]

Species	Dietary class[b]	Gizzards sampled	Occurrence (%)[c]	Count[d] $\bar{x} \pm$ SD	Count[d] Median	Mean size (mm)	Shape index[e]	Surface texture[e,f]
Ring-necked Pheasant (*Phasianus colchicus*)	G	37[g]	100	151 ± 190	88	2.3	2.0	3.3
Ring-necked Pheasant (*P. colchicus*)	O	4[g]	100	381 ± 258	430	1.7	1.8	3.1
Northern Bobwhite (*Colinus virginianus*)	O	75[g]	90	49 ± 106	12	1.8	1.8	3.1
Killdeer (*Charadrius vociferus*)	I	28[g]	93	8 ± 9	5	1.9	2.1	2.6
Rock Dove (*Columba livia*)	O	15	100	69 ± 43	60	2.3	2.0	3.3
Mourning Dove (*Zenaida macroura*)	G	40	68	10 ± 16	3	2.1	1.7	3.0
Yellow-billed Cuckoo (*Coccyzus americanus*)	I	9	44	3 ± 6	0	1.6	1.8	3.0
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	I	27[g]	57	31 ± 59	2	0.9	1.8	3.0
Eastern Kingbird (*Tyrannus tyrannus*)	I	29[g]	24	1 ± 4	0	1.3	1.9	2.7
Barn Swallow (*Hirundo rustica*)	I	23	22	1 ± 4	0	1.2	3.1	—
Horned Lark (*Eremophila alpestris*)	O	69[g]	99	11 ± 13	8	1.2	1.7	3.0
Blue Jay (*Cyanocitta cristata*)	O	20[g]	85	35 ± 42	15	1.6	2.1	2.8
American Crow (*Corvus brachyrhynchos*)	O	64[g]	53	49 ± 156	2	2.9	1.7	3.1
Cedar Waxwing (*Bombycilla cedorum*)	F	20	20	9 ± 40	0	0.3	1.7	2.9
Hermit Thrush (*Catharus guttatus*)	I	3	100	129 ± 163	54	0.3	1.7	3.0
Hermit Thrush (*C. guttatus*)	O	6	83	14 ± 17	6	0.3	1.8	2.7
American Robin (*Turdus migratorius*)	O	43[g]	44	12 ± 26	0	0.8	2.3	2.7
European Starling (*Sturnus vulgaris*)	O	56[g]	36	21 ± 85	0	1.0	1.8	2.7
House Wren (*Troglodytes aedon*)	I	7	57	3 ± 5	1	0.3	1.7	3.0
House Sparrow (*Passer domesticus*)	G	146[g]	98	281 ± 476	97	0.7	1.9	2.9
Yellow-rumped Warbler (*Dendroica coronata*)	I	5	0	0	0	—	—	—
Common Yellowthroat (*Geothlypis trichas*)	I	14	21	1 ± 2	0	0.3	1.8	2.8
Fox Sparrow (*Passerella iliaca*)	G	5	100	102 ± 88	93	0.5	2.0	3.1
Song Sparrow (*Melospiza melodia*)	O	14	93	14 ± 15	8	0.8	1.8	2.9
Savannah Sparrow (*Passerculus sandwichensis*)	G	21[g]	100	41 ± 102	20	1.0	2.0	3.0

TABLE 1
CONTINUED

Species	Dietary class[b]	Gizzards sampled	Occurrence (%)[c]	Count[d] $\bar{x} \pm$ SD	Count[d] Median	Mean size (mm)	Shape index[e]	Surface texture[ef]
Savannah Sparrow (*P. sandwichensis*)	O	5[g]	60	50 ± 80	22	0.7	1.9	3.4
American Tree Sparrow (*Spizella arborea*)	G	8	100	267 ± 212	203	0.4	1.9	3.1
Chipping Sparrow (*S. passerina*)	O	20	95	12 ± 16	7	0.9	2.1	2.9
Vesper Sparrow (*Pooecetes gramineus*)	O	125[g]	86	12 ± 14	8	0.9	1.8	3.1
Lark Sparrow (*Chondestes grammacus*)	O	5	100	42 ± 50	22	0.6	1.8	3.2
Dickcissel (*Spiza americana*)	O	28	25	4 ± 18	0	0.8	2.0	3.2
Northern Cardinal (*Cardinalis cardinalis*)	O	22[g]	73	40 ± 82	6	1.0	2.6	2.9
Indigo Bunting (*Passerina cyanea*)	O	21	81	35 ± 91	4	0.9	1.8	2.8
Northern Oriole (*Icterus galbula*)	O	5	0	0	0	—	—	—
Red-winged Blackbird (*Agelaius phoeniceus*)	O	82[g]	73	17 ± 61	4	1.1	1.8	3.0
Western Meadowlark (*Sturnella neglecta*)	I	9	44	2 ± 3	0	1.4	1.8	3.0
Common Grackle (*Quiscalus quiscula*)	O	47[g]	57	10 ± 21	1	0.9	2.2	2.9
Brown-headed Cowbird (*Molothrus ater*)	O	175[g]	52	10 ± 30	1	1.0	2.0	2.9

[a] Includes only those species for which ≥5 gizzards were sampled.
[b] Based on month of capture, using classification of DeGraaf et al. (1985). I = insectivore, G = granivore, O = omnivore, and F = frugivore.
[c] The percentage of gizzards in which grit particles were present.
[d] The number of grit particles per gizzard.
[e] See text for a description of how these values were derived.
[f] This variable was called "roundness" in Best and Gionfriddo (1991).
[g] These 17 species were used for intraspecific, gender comparisons of grit use.

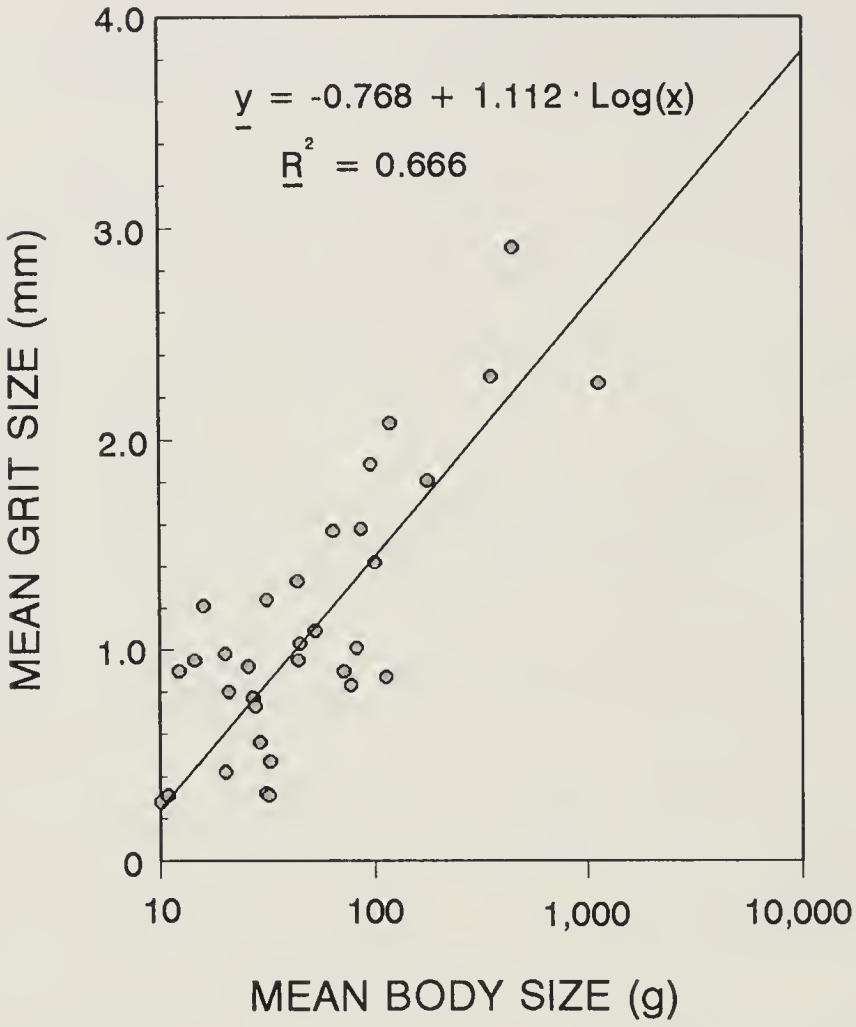

FIG. 1. Relationship between mean grit size and mean bird body mass. Body masses were obtained from Dunning (1993). Each point represents a species for which the contents of at least five gizzards were examined.

more angular (t = 2.38, 43 df, P = 0.022) grit than males. Female Ring-necked Pheasants and Horned Larks used smaller grit than males (pheasants: t = 2.48, 31 df, P = 0.019; larks: t = 2.10, 28 df, P = 0.045).

DISCUSSION

The most commonly proposed function of avian grit use is the facilitation of mechanical grinding and pulverization of food in the gizzard (Meinertzhagen 1964, Ziswiler and Farner 1972). Grit also may provide supplementary minerals, especially calcium (e.g., Korschgen 1964, Norris et al. 1975, Turner 1982). Avian grit use often varies with such factors as the bird's diet (e.g., Mott et al. 1972, Norris et al. 1975, Alonso 1985, Bishton 1986), age (Bartonek 1969, Verbeek 1970, Alonso 1985, Mayoh and Zach 1986), body size (Best and Gionfriddo 1991), and gender and

reproductive status (e.g., Harper 1964, Kopischke and Nelson 1966, May and Braun 1973, Pinowska and Kraśnicki 1985), as well as with the availability of suitable grit particles (Bump et al. 1947, Tindall 1973, Norris et al. 1975).

Diet is a major factor influencing avian grit use. Grit generally is found in the gizzards of most species that eat plant material (Farner 1960, Meinertzhagen 1964) and many that eat insects (e.g., Barlow et al. 1963, Jenkinson and Mengel 1970, Barrentine 1980, Mayoh and Zach 1986). Relatively large amounts of grit often are associated with diets consisting of hard, coarse materials, especially seeds and other plant parts (Meinertzhagen 1954, Farner 1960). Insectivores often use less grit than herbivorous or granivorous birds (Mott et al. 1972, Bishton 1986, Hogstad 1988), and frugivores typically use little grit (Meinertzhagen 1954, 1964). The amounts of grit needed by insectivores and granivores may depend on the hardness of the items consumed. The digestion of soft-bodied insect larvae, for example, may require relatively little grit, whereas the breakdown of hard-bodied insects (e.g., adult coleopterans) may require large amounts (Pinowska 1975, Gionfriddo and Best 1995). Grit-sized hard insect fragments (e.g., Bird and Smith 1964, Jenkinson and Mengel 1970, Mott et al. 1972) or hard seeds (e.g., Beer and Tidyman 1942, Sharp and McClure 1945, Lewin and Lewin 1984) are sometimes retained in the gizzard where they serve as grit substitutes by aiding in the mechanical grinding of softer foods. When such grit substitutes are present in gizzards, less grit is required. Hard insect parts or hard seeds were present in some of the gizzards we examined, and therefore, in some cases, our grit counts may underestimate the birds' need for grit.

Our finding no differences in adjusted mean grit size, mean grit shape, and mean grit surface texture among birds consuming different diets suggests that different foods may not require grit with different physical characteristics for adequate digestion. The characteristics of grit particles in birds' gizzards are influenced by avian preferences and aversions (Best and Gionfriddo 1994), the availability of grit particles with different characteristics (Bump et al. 1947, Tindall 1973, Norris et al. 1975), and rates of breakdown and passage of grit from the gizzards (Lienhart 1953, Korschgen et al. 1965, Vance 1971, Norris et al. 1975, Gionfriddo and Best 1995).

The large amounts of grit we observed in gizzards of Ring-necked Pheasants, American Tree Sparrows, and House Sparrows were not surprising because these species feed mainly on seeds on the ground. The relatively low grit counts and frequencies of occurrence of grit in gizzards of Eastern Kingbirds, Barn Swallows, and Cedar Waxwings were expected because these species feed on insects or fruits, aerially or in trees.

The other species that tended to use little or no grit (Common Yellowthroat, Yellow-rumped Warbler, Northern Oriole) also glean insects in trees or shrubs. The finding that Dickcissels used little grit on their North American breeding grounds is consistent with Zimmerman's (1963) report that wintering Dickcissels in central America used relatively large amounts of grit, but that breeding birds in Illinois used little. Zimmerman (1963) attributed the difference to the Dickcissels' heavier use of insects in North America and seeds in central America. Field studies of other avian species that shift diets seasonally also have documented corresponding shifts in grit use (Bishton 1986, Hogstad 1988, Gionfriddo and Best 1995). Investigation of seasonal patterns of grit use by additional species that shift diets seasonally would further clarify the relationship between grit use and diet.

The observed log-linear relationship between mean grit size and bird body mass is similar to that reported for 19 avian species collected mainly in the Midwest during the breeding season (Best and Gionfriddo 1991). Augmenting the earlier sample by including birds representing many additional avian taxa, geographical locations, and seasons did not substantially alter the linear model describing this relationship. The lack of a strong relationship between mean grit size and mean grit count for most (22 of 33) species we tested differs from the results of other field (Myrberget et al. 1975, Norris et al. 1975, Alonso 1985, Best and Gionfriddo 1991) and laboratory (McCann 1939, Smith 1960, Gionfriddo and Best 1995) studies which found that the larger the grit particles, the fewer were present in gizzards. The current finding is consistent, however, with the results of a diet experiment with captive House Sparrows (Gionfriddo and Best 1995).

Grit use by males and females often is reported to be similar (e.g., Alonso 1985, Norman and Brown 1985, Garcher and Carroll 1991, Gionfriddo and Best 1995). When differences exist, they sometimes are due to differences in body size (Rajala 1958, Pulliainen 1979, Norman and Mumford 1985) or to females' increased calcium requirements during egg laying (Sadler 1961, Harper 1964, Taylor 1970). Females may greatly increase their consumption of grit during the egg-laying period (Pinowska and Kraśnicki 1985), and/or they may selectively consume calcium-rich grit particles (Harper 1964, Korschgen 1964, Kopischke and Nelson 1966). Such reproduction-related changes in grit use (and gender differences that result from them) may be short-lived (Pinowska and Kraśnicki 1985), however, and therefore probably would not have been detectable in our study.

In addition to demonstrating the importance of diet and body size as factors affecting avian grit use, our study shows that grit use is widespread

among birds, both taxonomically and geographically. Moreover, although the collection of birds for this research was not limited geographically or temporally to areas or seasons of application of granular pesticides, our results nonetheless have important implications for the design and use of such products. Granular pesticides are applied to millions of hectares of agricultural crops in North America each year (U.S. Dept. Agric. 1992). Many of these pesticides are acutely toxic to birds (Balcomb et al. 1984, Hill and Camardese 1984), and one potential route of avian exposure is consumption of granules as a source of grit. Our results indicate that, if this is an important route of avian exposure to granular pesticides, then in pesticide-treated areas granivorous birds (including such important game species as the Ring-necked Pheasant and Northern Bobwhite) may have a relatively high risk of exposure because they use more grit than birds that eat other foods. Our results confirm that altering granule size to reduce avian risk is not likely to be effective. The wide range of grit sizes used by birds, and the extensive interspecific overlap in grit sizes result in there being no "safe" granule size that would be infrequently used by birds, given the upper and lower limits to pesticide granule size imposed by other factors, such as human safety and ease of application.

ACKNOWLEDGMENTS

We thank K. L. Andersen, K. K. Aulwes, B. M. Ballard, C. Best, J. D. Best, N. Best, J. R. Gionfriddo, J. M. Grady, D. S. Huntrods, L. D. Igl, A. L. Linville, F. D. Zenitsky, and G. D. Zenitsky for assisting with laboratory work and data tabulation. We are grateful to those who provided or collected birds for our study, especially J. J. Dinsmore, B. J. Giesler, L. D. Igl, D. W. DeGeus, D. S. Huntrods, and G. M. Booth. We appreciate the cooperation of state and federal agencies in granting permission for collection of birds. We thank C. E. Braun, J. J. Dinsmore, E. E. Klaas, J. L. Sell, K. C. Shaw, D. W. White, and C. R. Blem for reviewing earlier drafts of the manuscript and offering helpful suggestions. Funding was provided by Miles, Inc., Rhône-Poulenc, American Cyanamid, and Dow Elanco. This is Journal Paper No. J-16181 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Project 2168.

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Wilson Bull., 108(4), 1996, pp. 697–711

RED-COCKADED WOODPECKER NESTING SUCCESS, FOREST STRUCTURE, AND SOUTHERN FLYING SQUIRRELS IN TEXAS

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Abstract.—For several decades general opinion has suggested that southern flying squirrels (*Glaucomys volans*) have a negative effect on Red-cockaded Woodpeckers (*Picoides borealis*) through competition for cavities and egg/nestling predation. Complete removal of hardwood trees from Red-cockaded Woodpecker cavity tree clusters has occurred on some forests because southern flying squirrel abundance was presumed to be associated with the presence and abundance of hardwood vegetation. In some locations, southern flying squirrels have been captured and either moved or killed in the name of Red-cockaded Woodpecker management. We determined southern flying squirrel occupancy of Red-cockaded Woodpecker cavities in loblolly (*Pinus taeda*)–shortleaf (*P. echinata*) pine habitat (with and without hardwood midstory vegetation) and longleaf pine (*P. palustris*) habitat (nearly devoid of hardwood vegetation) during spring, late summer, and winter during 1990 and 1991. Flying squirrel use of Red-cockaded Woodpecker cavities was variable and was not related to presence or abundance of hardwood vegetation. Woodpecker nest productivity was not correlated with flying squirrel use of woodpecker cavities within clusters. In addition, we observed six instances where Red-cockaded Woodpeckers successfully nested while flying squirrels occupied other cavities in the same tree. Our results suggest that complete removal of hardwoods from woodpecker cluster areas in loblolly and shortleaf pine habitat may not provide benefits to the woodpeckers through reduction of flying squirrel numbers. Reduction of hardwood midstory around cavity trees, however, is still essential because of the woodpecker's apparent innate intolerance of hardwood midstory foliage. *Received 3 Nov. 1995, accepted 21 Mar. 1996.*

The Red-cockaded Woodpecker (*Picoides borealis*) is a cooperative breeder that lives in family groups composed of a breeding pair and frequently one to several helpers (Ligon 1970, Walters et al. 1988, Walters 1990). The activities of the group center around a cluster of cavity trees composed of living pines that contain one to several cavities and cavity starts. Cavities are excavated into the heartwood of pines that typically are infected with red heart fungus (*Phellinus pini*) (Conner and Locke 1982, Hooper 1988, Hooper et al. 1991, Rudolph et al. 1995). Cavity excavation in Texas requires an average of 1.8 y in loblolly pines (*Pinus taeda*), 2.4 y in shortleaf pines (*P. echinata*), and 6.3 y in longleaf pines (*P. palustris*) (Conner and Rudolph 1995). Pines selected for cavities in Texas usually exceeded 90 years of age (Conner and O'Halloran 1987,

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Rudolph and Conner 1991). The Red-cockaded Woodpecker is a keystone species of the fire-climax, southern pine ecosystems in that they are the primary species to excavate cavities in an otherwise cavity-barren environment relative to hardwood ecosystems (Conner and Rudolph 1995). Thus, the cavities that take Red-cockaded Woodpeckers a long time to create tend to be in relatively high demand by other cavity-using species (Dennis 1971, Rudolph et al. 1990b, Loeb 1993).

As cavities near completion, Red-cockaded Woodpeckers peck shallow excavations, termed resin wells, around their cavity entrances. Continued pecking at resin wells causes a copious flow of resin down the bole of the pine (Ligon 1970). Woodpeckers also scale loose bark from the bole of the cavity tree and nearby pines. Although bark scaling and resin flow usually deters climbing by rat snakes (*Elaphe obsoleta*) (Jackson 1974, Rudolph et al. 1990a), the resin barrier does not deter southern flying squirrels (*Glaucomys volans*) which are frequent users of cavities with unenlarged entrances that are also preferred by Red-cockaded Woodpeckers (Rudolph et al. 1990b, Loeb 1993).

Past studies have indicated a negative association between Red-cockaded Woodpeckers and the density of hardwood midstory and understory (Hopkins and Lynn 1971, Van Balen and Doerr 1978, Hovis and Labisky 1985, Conner and Rudolph 1989, Loeb et al. 1992). This has lead to widespread management programs that remove all hardwood vegetation from Red-cockaded Woodpecker cavity tree cluster areas (Conner and Rudolph 1991b). Although the negative effect of hardwood vegetation on Red-cockaded Woodpeckers is well documented, the mechanism that causes this negative relationship is poorly understood. One proposed mechanism for the hardwood effect is that southern flying squirrels, a potential competitor for Red-cockaded Woodpecker cavities, are dependent on hardwood midstory foliage. However, flying squirrels appear to prefer hardwood vegetation primarily as understory cover and as a food source (Bendel and Gates 1987). Contrary to popular belief, southern flying squirrels may avoid areas with dense midstory foliage because it interferes with flight paths between boles of larger pines (Bendel and Gates 1987). The influence of plant species composition and midstory and understory foliage densities in pine forests on southern flying squirrel abundance is not fully understood. To date, no published studies have demonstrated that southern flying squirrels have a negative effect on Red-cockaded Woodpecker populations, yet management programs that include removal of southern flying squirrels from cavities and euthanasia (Gaines et al. 1995) are becoming more widespread.

Several species of woodpeckers enlarge Red-cockaded Woodpecker cavity entrance tunnels by excavation and use the cavities (Conner et al.

1991, Neal et al. 1992). Some of these species, e.g., Pileated (*Dryocopus pileatus*) and Red-bellied (*Melanerpes carolinus*) woodpeckers, are considered to be primarily associated with hardwood forests (Reller 1972, Conner et al. 1975). Metal plates that restrict the entrance diameter of Red-cockaded Woodpecker cavities (Carter et al. 1989) have been developed for placement over enlarged cavities in hopes that some currently unsuitable cavities can be rehabilitated and on unenlarged cavities to prevent enlargement. Although these plates may prevent further damage by larger species of woodpeckers, they will not deter the use of cavities by southern flying squirrels or other small species of woodpeckers which prefer smaller entrances.

The competitive impact of southern flying squirrels on Red-cockaded Woodpeckers is largely hypothetical. If a detrimental impact is occurring, it may be exacerbated in small declining Red-cockaded Woodpecker populations such as those in eastern Texas that are also stressed by other factors such as isolation and forest fragmentation (Conner and Rudolph 1989, 1991a).

Our objectives were to (1) determine the availability and use of Red-cockaded Woodpecker cavities during the nesting, late-summer, and winter seasons, (2) evaluate southern flying squirrel use of cavities in relation to species composition and structure of vegetation, and (3) explore possible negative effects of southern flying squirrels on Red-cockaded Woodpecker breeding success.

STUDY AREAS AND METHODS

The study was conducted on the Angelina (62,423 ha; 31°15′N, 94°15′W) and Davy Crockett (65,329 ha; 31°21′N, 95°07′W) National Forests from March 1990 to October 1991. We examined 11 Red-cockaded Woodpecker cavity clusters in open longleaf pine habitat, 10 clusters in loblolly-shortleaf pine habitat with all hardwood vegetation removed in the cluster area, and seven clusters in loblolly–shortleaf pine habitat with extensive hardwood vegetation present during 1990. We suspected that different seasons of the year may impose varying levels of competition for cavities. The breeding season (spring) is likely to be a season of potentially elevated competition, and competition at that time can decrease breeding success. The late summer season may also be a critical period because new young have fledged and are searching for cavities for nocturnal roost sites. We sampled cavity occupants during winter to examine the possibility that thermal stress during the colder months may lead to increased demand for cavities.

We climbed approximately 230 cavity trees using Swedish climbing ladders and examined them for occupancy during spring (April to May) of 1990 and 1991, late summer (August to October) of 1990 and 1991, and winter of 1990–1991 (December 1990 to February 1991). Only a few cavity trees were not climbed because of safety factors during each climbing season. Such trees were typically small-diameter, old, inactive cavity trees that were primarily hollow shells and whose cavities were of no use to Red-cockaded Woodpeckers for cavities. We lowered a small, high intensity light into each cavity chamber, examined contents with an oval mechanics mirror mounted on an extendable handle, and identified and

counted cavity occupants. Often more than one southern flying squirrel was present in a cavity. When this occurred, a coat hanger wire (with the end bent around to prevent injury) was placed into the cavity and flying squirrels lifted out for counting. We used presence of chewed pine needles and fresh flying squirrel feces as an indicator of flying squirrel use. Unchewed pine needles in an enlarged cavity indicated use by fox squirrels (*Sciurus niger*). Cavity trees that were being simultaneously used by both southern flying squirrels and Red-cockaded Woodpeckers (in two different cavities) were examined closely during the woodpecker nesting season to determine woodpecker fledging success and during other seasons to detect cavity usurpation by flying squirrels. We measured the entrance diameters of cavities and monitored cavities with restrictors in each cluster studied. Based on previous studies (Rudolph et al. 1990b), cavities were divided into those suitable for Red-cockaded Woodpecker use (entrance diameters <7 cm in diameter) and those too enlarged to be acceptable to Red-cockaded Woodpeckers (entrances >7 cm in diameter).

We measured reproductive success of Red-cockaded Woodpeckers in each cluster by determining the number of young fledged from nest cavities. Young were counted at 8, 20, and 23 days of age in each nest tree. Clusters were visited within a week of fledging to determine how many of the nestlings observed on day 23 successfully fledged. We also visited each cluster during August and September to determine number of surviving young. We made dawn and dusk visits to each woodpecker group to verify roost locations, band woodpeckers, and determine number of members in each family group during each climbing season. We also determined the number of Red-cockaded Woodpeckers roosting outside of cavities in the open.

Vegetation measured in each cavity tree cluster (six points per cluster) included basal area of overstory and midstory pines and hardwoods using a one-factor metric prism, height of midstory and understory vegetation using a clinometer, canopy closure using a 4-cm diameter by 12 cm hollow tube, and foliage density of vegetation from the ground to 1 m, and 1 m to 2 m using a density board as described by MacArthur and MacArthur (1961). By spring 1991, the seven clusters which had a well-developed hardwood midstory during the first year of the study had received midstory treatment. All hardwood vegetation was removed from these seven clusters during the 1990–1991 winter giving them the same structural appearance as the 10 clusters in loblolly–shortleaf habitat that were initially without hardwoods.

For each cavity tree cluster during each season we calculated the percentage of unenlarged cavities occupied by southern flying squirrels and those occupied by Red-cockaded Woodpeckers. Analysis of variance and Duncan's multiple range test were used to test for differences in flying squirrel and Red-cockaded Woodpecker use of cavities among habitat treatments during each season ($P = 0.05$). We related fledging success with the proportion of unenlarged cavities (all unenlarged and available unenlarged cavities) occupied by flying squirrels with Spearman correlations (r_s, $P = 0.05$).

RESULTS

Vegetation characteristics of cavity tree clusters.—Vegetation within the three treatments differed distinctly during the first year of the study (1990). Red-cockaded Woodpecker cavity tree clusters in longleaf pine habitat were nearly devoid of any hardwood vegetation or understory and midstory foliage except for grasses and forbs (Table 1), and the absence of hardwoods extended well beyond the boundaries of cluster areas. This was not the case in clusters located in loblolly–shortleaf pine habitat.

TABLE 1

VEGETATIVE CHARACTERISTICS (MEAN ± SD) OF RED-COCKADED WOODPECKER CLUSTER AREAS WHERE CAVITY OCCUPANTS WERE MONITORED IN LONGLEAF PINE, LOBLOLLY-SHORTLEAF PINE WITH NO MIDSTORY, LOBLOLLY-SHORTLEAF PINE WITH MIDSTORY PRESENT (PRE-TREATMENT 1990) AND MIDSTORY REMOVED (POST-TREATMENT 1991) ON THE ANGELINA AND DAVY CROCKETT NATIONAL FORESTS IN EASTERN TEXAS

Habitat variable	Longleaf pine (N = 11)	Loblolly-shortleaf no midstory (N = 10)	Loblolly-shortleaf with midstory (N = 7)	Loblolly-shortleaf midstory removed (N = 7)
Overstory pine basal area[a] (m^2/ha)	14.0 (6.6)[b]	12.7 (3.5)[b]	10.9 (4.1)[c]	13.6 (3.7)[b]
Overstory hardwood basal area (m^2/ha)	0.1 (0.2)[b]	0.0 (0.0)[b]	1.0 (4.3)[c]	0.0 (0.3)[b]
Midstory pine basal area (m^2/ha)	0.2 (0.5)[b]	0.5 (1.2)[b]	1.8 (3.0)[c]	0.3 (0.9)[b]
Midstory hardwood basal area (m^2/ha)	0.0 (0.0)[b]	0.1 (0.3)[b]	1.7 (1.7)[c]	0.2 (0.6)[b]
Canopy closure (%)	46.3 (26.1)[b]	51.5 (16.9)[bc]	55.8 (19.8)[c]	53.5 (15.8)[bc]
Overstory height (m)	23.1 (2.0)[b]	24.8 (2.8)[c]	27.0 (3.7)[d]	25.3 (1.5)[c]
Midstory height (m)	6.7 (5.4)[b]	3.3 (5.4)[c]	12.4 (4.5)[d]	3.3 (7.3)[c]
Understory height (m)	1.9 (0.9)[b]	1.6 (0.6)[c]	2.0 (0.8)[b]	1.5 (0.5)[c]
Foliage density 0–1 m (cm^2/m^3)	0.2 (0.2)[b]	0.3 (0.1)[b]	0.3 (0.2)[b]	0.5 (0.7)[c]
Foliage density 1–2 m (cm^2/m^3)	0.1 (0.1)[bc]	0.1 (0.1)[b]	0.2 (0.1)[d]	0.1 (0.2)[cd]

[a] Common letters indicate nonsignificant differences (ANOVA, Duncan's multiple range test [$P = 0.05$]).

Clusters in habitat where hardwoods had recently been removed were quite similar to longleaf habitat in the actual cluster area (Table 1), however, a virtual wall of hardwood midstory foliage was encountered at the edges of each cluster where midstory removal and thinning of overstory pines had ceased. Clusters that had not yet received hardwood removal treatment still had substantial hardwoods in the overstory, midstory, and understory (Table 1). During the winter of 1990–1991, hardwoods and midstory trees in the seven untreated clusters were removed, changing those clusters into a vegetative condition similar to the loblolly–shortleaf clusters that had received midstory treatment prior to the study (Table 1).

Faunal use of Red-cockaded Woodpecker cavities.—A variety of vertebrates and invertebrates were observed using Red-cockaded Woodpecker cavities during the study. Although observed in cavities infrequently, American Kestrels (*Falco sparverius*), Eastern Screech-Owls (*Otus asio*), Pileated Woodpeckers, Wood Ducks (*Aix sponsa*), and fox squirrels typically used cavities which had both the entrance and cavity chamber enlarged. Eastern Screech-Owls were observed in three cavities with entrances <7 cm in diameter, but the entrances of these three cavities had

been slightly enlarged and were between 6.5 and 7 cm in diameter. Red-bellied Woodpeckers are known to conflict with Red-cockaded Woodpeckers over cavities (Neal et al. 1992, Kappes and Harris 1995) but were observed using unenlarged cavities only once during spring 1991 and on four occasions during winter.

Mud-daubers (Sphecidae) were typically found in inactive cavities. Their mud chambers were tolerated or pecked off when Red-cockaded Woodpeckers began to use a cavity containing mud-dauber nests. The presence of mud-daubers or their nests did not appear to interfere with Red-cockaded Woodpecker use of cavities. However, the presence of paper wasps (Vespidae), particularly large nests, and honey bees (*Apis mellifera*) did prevent Red-cockaded Woodpecker use of cavities. Broad-headed skinks (*Eumeces laticeps*), five-lined skinks (*E. fasciatus*), and gray tree frogs (*Hyla versicolor\chrysoscelis*) were observed occasionally within inactive enlarged and unenlarged cavities.

Southern flying squirrel use of woodpecker cavities.—Red-cockaded Woodpeckers preferred unenlarged cavities (Table 2); they used cavities with greatly enlarged entrances (≥7 cm) in only two instances, both during late summer 1990. As previously noted by Rudolph et al. (1990b) and Loeb (1993), southern flying squirrels also prefer entrance diameters <7 cm. Thus, the southern flying squirrel exhibited extensive overlap in cavity use with Red-cockaded Woodpeckers; it was observed in relatively high numbers and also used primarily unenlarged cavities (Table 2). In most clusters, however, empty unenlarged and enlarged cavities were available throughout the year for either Red-cockaded Woodpeckers or flying squirrels to use (Tables 2, 3).

Southern flying squirrel use of Red-cockaded Woodpecker cavities during the woodpecker breeding season (spring) was high, but dwindled greatly by late summer during both 1990 and 1991 (Table 2). The number of cavities used by Red-cockaded Woodpeckers was somewhat higher during late summer than during the breeding season. Red-cockaded Woodpeckers were present in greater numbers in the late summer because young woodpeckers had recently fledged from nest cavities and many were now roosting in cavities.

We detected very few significant differences in the percentage of unenlarged cavities used by Red-cockaded Woodpeckers and southern flying squirrels among habitat treatments (Table 3). During spring 1990 southern flying squirrels used unenlarged Red-cockaded Woodpecker cavities at a higher frequency in longleaf pine habitat than in loblolly–shortleaf habitat where hardwood midstory vegetation was absent (Table 3). During spring 1991 the percentage of empty unenlarged cavities in loblolly–shortleaf pine habitat without midstory was significantly lower than in longleaf

TABLE 2

NUMBER OF UNENLARGED (ENTRANCE <7 CM DIAMETER) AND ENLARGED (ENTRANCE ≥7 CM DIAMETER) RED-COCKADED WOODPECKER CAVITIES OCCUPIED BY RED-COCKADED WOODPECKERS AND SOUTHERN FLYING SQUIRRELS IN THREE HABITAT TREATMENTS ON THE ANGELINA AND DAVY CROCKETT NATIONAL FORESTS IN EASTERN TEXAS

	Loblolly-shortleaf pine					
	With midstory pre-removal		Without midstory		Longleaf pine	
Cavity occupant	<7 cm	≥7 cm	<7 cm	≥7 cm	<7 cm	≥7 cm
Spring 1990 sample sizes	(N = 49)	(N = 15)	(N = 31)	(N = 20)	(N = 52)	(N = 21)
Red-cockaded Woodpecker	21	0	22	0	18	0
Flying squirrel/no. of squirrels	18/55	1/2	9/25	2/8	28/77	2/3
Empty cavities	7	4	8	13	2	7
Summer 1990 sample sizes	(N = 52)	(N = 11)	(N = 45)	(N = 18)	(N = 56)	(N = 23)
Red-cockaded Woodpecker	28	0	23	1	23	1
Flying squirrel/no. of squirrels	6/8	1/1	4/5	0	4/7	0
Empty cavities	14	7	15	15	24	18
Spring 1991 sample sizes	(N = 49)	(N = 13)	(N = 65)	(N = 12)	(N = 69)	(N = 23)
Red-cockaded Woodpecker	13	0	27	0	22	0
Flying squirrel/no. of squirrels	15/45	1/4	24/65	2/4	22/77	4/15
Empty cavities	13	4	10	5	17	11
Summer 1991 sample sizes	(N = 49)	(N = 13)	(N = 65)	(N = 13)	(N = 67)	(N = 26)
Red-cockaded Woodpecker	23	0	37	0	37	0
Flying squirrel/no. of squirrels	10/16	1/1	5/7	0	11/24	5/11
Empty cavities	11	6	15	10	19	18
Winter 1990-1991 sample sizes	(N = 51)	(N = 14)	(N = 55)	(N = 18)	(N = 52)	(N = 21)
Red-cockaded Woodpecker	17	0	30	0	26	0
Flying squirrel/no. of squirrels	13/31	1/2	7/22	1/2	10/30	1/5
Empty cavities	16	10	9	9	21	15

TABLE 3

PERCENTAGE OF UNENLARGED CAVITIES WITHIN EACH CLUSTER OCCUPIED BY RED-COCKADED WOODPECKERS BY SOUTHERN FLYING SQUIRRELS, OR EMPTY (MEAN ± SD) IN LOBLOLLY-SHORTLEAF PINE HABITAT WITHOUT HARDWOOD MIDSTORY VEGETATION (N = 10), LOBLOLLY-SHORTLEAF PINE HABITAT WITH HARDWOOD MIDSTORY VEGETATION (PRE- AND POST-REMOVAL, N = 7), AND LONGLEAF PINE HABITAT (N = 11) IN EASTERN TEXAS

	Habitat treatment							
	Loblolly-shortleaf without midstory		Loblolly-shortleaf with midstory (pre-removal)		Loblolly-shortleaf post midstory removal		Longleaf	
Variable	$\bar{x}$[a]	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Spring 1990								
Red-cockaded (%)	56.4[b]	26.3	43.5[b]	24.6			50.3[b]	33.7
Flying squirrel (%)	16.9[b]	18.8	38.8[bc]	28.0			44.8[c]	31.0
Empty (%)	14.7[b]	16.6	14.6[b]	18.3			3.8[b]	8.6
Spring 1991								
Red-cockaded (%)	48.2[b]	17.2			29.5[b]	14.7	35.5[b]	26.3
Flying squirrel (%)	41.6[b]	14.8			38.4[b]	15.0	28.5[b]	20.9
Empty (%)	7.2[b]	13.0			27.2[c]	15.1	30.9[c]	14.7
Summer 1990								
Red-cockaded (%)	64.0[b]	34.8	60.8[b]	25.8			46.9[b]	30.7
Flying squirrel (%)	7.0[b]	9.5	14.4[b]	14.1			6.1[b]	11.2
Empty (%)	25.0[b]	23.8	21.4[b]	24.5			46.3[b]	28.4
Summer 1991								
Red-cockaded (%)	60.4[b]	17.5			49.7[b]	24.9	58.8[b]	20.1
Flying squirrel (%)	7.8[b]	10.4			23.0[b]	23.2	19.6[b]	13.2
Empty (%)	26.2[b]	15.1			25.0[b]	10.3	21.6[b]	21.3
Winter 1990–1991								
Red-cockaded (%)	62.8[b]	25.2			38.2[c]	12.6	47.1[bc]	26.3
Flying squirrel (%)	16.3[b]	19.3			25.7[b]	12.5	19.4[b]	15.2
Empty (%)	18.9[b]	21.2			27.8[b]	11.4	28.1[b]	22.9

[a] Common superscript letters following means indicate nonsignificant differences among habitat treatments (ANOVA, Duncan's multiple range test, $P = 0.05$).

pine or loblolly–shortleaf pine from which midstory had been recently removed (Table 3). Southern flying squirrel use of Red-cockaded Woodpecker cavities was not related to the presence or absence of hardwood midstory (Table 3). Thus, treatment specific and annual use of cavities by flying squirrels appears to be minimally affected by hardwood midstory abundance.

Southern flying squirrel use of cavities in the loblolly–shortleaf habitat with midstory was greater than their use of loblolly–shortleaf habitat without hardwood vegetation during spring 1990, although not significantly

TABLE 4

NUMBER OF RED-COCKADED WOODPECKERS ROOSTING IN THE OPEN DURING SPRING AND LATE SUMMER 1990 AND 1991 IN LOBLOLLY-SHORTLEAF PINE HABITAT WITHOUT HARDWOOD MIDSTORY VEGETATION (N = 10 CLUSTERS), WITH HARDWOOD MIDSTORY VEGETATION (PRE- AND POST-HARDWOOD REMOVAL, N = 7 CLUSTERS), AND LONGLEAF PINE HABITAT (N = 11 CLUSTERS) IN EASTERN TEXAS

	Habitat treatment		
	Loblolly-shortleaf without midstory	Loblolly-shortleaf with midstory	Longleaf
Season	No. woodpeckers	No. woodpeckers	No. woodpeckers
Spring 1990	1	1[a]	6
Summer 1990	3	5[a]	4
Spring 1991	1	3[b]	0
Summer 1991	2	2[b]	2

[a] Pre-midstory removal treatment within these clusters.
[b] Post-midstory removal treatment within cluster areas completed during winter 1990–1991.

so (Table 3). However, the percentage of unenlarged cavities used by flying squirrels remained the same during spring 1991 even though hardwood midstory vegetation had been removed (Table 3). Flying squirrel use of unenlarged cavities increased in the loblolly–shortleaf area without midstory even though no habitat alteration occurred (Table 3). Both the percentage of cavities used by flying squirrels and the abundance of flying squirrels counted in Red-cockaded Woodpecker cavities decreased between spring and late summer in 1990 and 1991 (Table 2, 3). We did not make a detailed survey of the crowns of nearby pines and hardwoods in the woodpecker cluster areas, but strongly suspect that flying squirrels were spending the hot, late summers in leaf nests rather than woodpecker cavities, as also observed by Muul (1974).

During winter, the percentage of unenlarged cavities and available unenlarged cavities used by southern flying squirrels was relatively similar in all habitat treatments (Table 3). Empty unenlarged cavities were readily available in clusters in all habitat treatments during winter, suggesting that cavity availability did not create a competitive problem for Red-cockaded Woodpeckers during winter.

Extra-cavity roosting by woodpeckers.—Extra-cavity roosting as described by Hooper and Lennartz (1983) is a possible indicator of insufficient cavity availability for Red-cockaded Woodpeckers. In general, very few Red-cockaded Woodpeckers were observed roosting in the open (Table 4). Typically, when Red-cockaded Woodpeckers roosted in the open, there were empty cavities available within their cluster areas. Spring 1990 in the longleaf pine habitat appeared to be exceptional in this regard.

With the exception of longleaf pine habitat in spring 1990, Red-cockaded Woodpeckers appeared to roost in the open more during late summer than during the breeding season (Table 4). Flying squirrels were very abundant during spring 1990 in the longleaf habitat (Table 2) and empty cavities were few, suggesting that a few Red-cockaded Woodpeckers may have been forced temporarily to roost in the open. Many recently fledged young Red-cockaded Woodpeckers did not roost in cavities during the late summer. Because many unenlarged empty cavities were available for these woodpeckers to use during late summer, roosting in the open appears to be voluntary and may have been in response to the typical high air temperatures during August and September.

Red-cockaded Woodpecker fledging success.—We examined Red-cockaded Woodpecker fledging success to explore the possibility that interactions with southern flying squirrels reduced woodpecker nest productivity. Because southern flying squirrel use of woodpecker cavities was uniformly high over all habitat treatments and years, our ability to evaluate the influence of squirrel use of cavities on fledging success through comparisons across habitats was limited.

Fledging success was slightly higher in loblolly–shortleaf habitat with hardwood vegetation (pre-hardwood removal) than in the loblolly–shortleaf habitat without hardwood vegetation during 1990 (Fig. 1). Fledging success remained somewhat higher in these cluster areas in 1991 (post-treatment) even though the hardwood vegetation had been removed prior to the 1991 breeding season. Longleaf pine habitat, relatively devoid of hardwood vegetation, and often considered the premiere habitat for the woodpecker, had a slightly lower fledging success than either loblolly–shortleaf habitats during both 1990 and 1991 (Fig. 1). Excluding nests where eggs failed to hatch, we failed to detect any significant differences in fledging success among habitat treatments (Kruskal-Wallis χ^2 approximation, $\chi^2 = 1.42$, $P = 0.49$).

We compared the proportion of all unenlarged cavities used by flying squirrels and the proportion of available unenlarged cavities (open cavities not used by Red-cockaded Woodpeckers) that contained flying squirrels with woodpecker fledging success (Fig. 1). During both 1990 and 1991 we observed no relationship between southern flying squirrel occupancy and habitat condition (abundance of hardwood midstory) or Red-cockaded Woodpecker fledging success. Red-cockaded Woodpecker fledging success per habitat treatment during the two breeding seasons (N = 6) was not correlated with the percentage of all unenlarged cavities occupied by southern flying squirrels ($r_s = -0.08$, $P = 0.87$) or the percentage of available unenlarged cavities (those not used by Red-cockaded Woodpeckers) occupied by southern flying squirrels ($r_s = -0.46$, $P = 0.35$). If

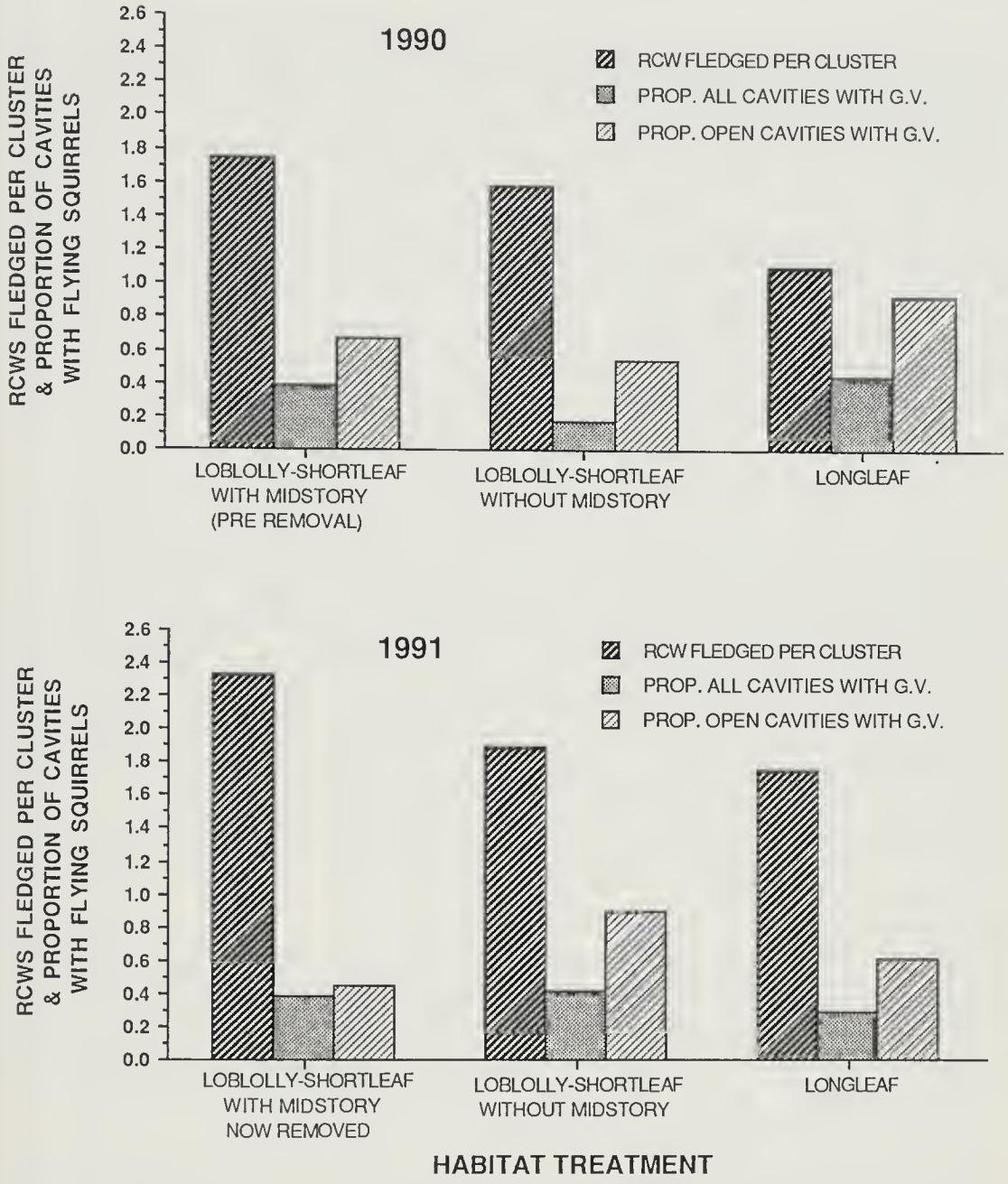

FIG. 1. Comparisons of Red-cockaded Woodpecker fledging success with the proportion of all unenlarged Red-cockaded Woodpecker cavities occupied by southern flying squirrels (*Glaucomys volans,* G. V.) and available unenlarged cavities (those not used by Red-cockaded Woodpeckers) occupied by southern flying squirrels in loblolly-shortleaf pine habitat with hardwood midstory present (pre- and post-hardwood removal), loblolly-shortleaf pine habitat without hardwood midstory throughout the study, and longleaf pine habitat during the 1990 and 1991 breeding seasons on the Angelina and Davy Crockett National Forests in eastern Texas.

clusters are treated as the sample unit (N = 44), fledging success is still not correlated with either the percentage of all unenlarged cavities occupied by flying squirrels ($r_s = -0.18$, $P = 0.23$), or the percentage of available unenlarged cavities occupied by flying squirrels ($r_s = -0.11$, $P = 0.48$).

Potential for flying squirrel predation on woodpeckers.—During our 2 year study we observed 6 instances where Red-cockaded Woodpeckers nested and produced young in cavities while southern flying squirrels were occupying other cavities in the same pine tree. In only one instance were eggs lost (to unknown causes), but the woodpeckers renested and successfully fledged young from the same cavity. Young fledged successfully from all five of the other nest cavities.

DISCUSSION

Competition between flying squirrels and woodpeckers.—Our observations in eastern Texas suggest a minimal competitive impact of southern flying squirrels on Red-cockaded Woodpeckers. Because we did not measure woodpecker fledging success over a wide range of flying squirrel abundance, however, our results may not be definitive. Competition from southern flying squirrels in Texas is likely transient and occurs as isolated events during ecological "bottle-necks." If such competition occurs at all in eastern Texas, the effects are subtle rather than overwhelming. The effect of southern flying squirrels on any healthy woodpecker population is probably minimal to non-existent.

Specifically, we have not seen (1) a relationship between woodpecker fledging success and flying squirrel use of cavities, (2) Red-cockaded Woodpeckers forced to roost in the open because of a squirrel-caused shortage of unenlarged cavities, or (3) regular squirrel predation on Red-cockaded Woodpecker eggs and young even when both woodpeckers and flying squirrels occupied the same cavity tree.

Relationships among woodpeckers, squirrels, and hardwood vegetation.—We did not observe a strong relationship between southern flying squirrel abundance and presence of hardwood vegetation. Flying squirrels were common in cavities in longleaf pine habitat with almost no hardwood vegetation. This finding, however, does not negate the necessity to reduce hardwood vegetation within woodpecker cluster areas. Past studies have clearly demonstrated the negative effects of excessive hardwood midstory on woodpecker populations (Van Balen and Doerr 1978, Hovis and Labisky 1985, Conner and Rudolph 1989, Loeb et al. 1992). Thus, we strongly urge that *reduction* (not elimination) of hardwood vegetation within Red-cockaded Woodpecker cluster areas be continued.

Our results indicate that complete or partial removal of all hardwoods

will likely not affect the use of Red-cockaded Woodpecker cavities by southern flying squirrels. What our study suggests is that southern flying squirrels are not the cause of harmful effects on Red-cockaded Woodpeckers associated with the presence of hardwood vegetation within their cluster areas. As we have suggested before (Conner and Rudolph 1991b), Red-cockaded Woodpeckers may have an innate avoidance of areas with extensive hardwood vegetation as a result of their adaptation to the southern fire-climax pine ecosystem. A selective advantage may accrue for Red-cockaded Woodpecker pairs that avoid habitat with abundant hardwood vegetation because such areas may support greater numbers of other species of woodpeckers that can easily out-compete Red-cockaded Woodpeckers for cavities or destroy the cavities they excavate. Another possible reason why Red-cockaded Woodpeckers have an aversion to hardwoods is that they may provide predators access to cavities (Walters 1990).

We saw no negative effect of southern flying squirrels on Red-cockaded Woodpeckers, nor have any other studies demonstrated such an effect. We strongly discourage removal and euthanasia of southern flying squirrels in woodpecker clusters because of the complete lack of evidence that it would benefit Red-cockaded Woodpeckers. If removal of southern flying squirrels is deemed necessary, it should be based on site-specific data that statistically demonstrates a severe competitive problem. In such instances, control of flying squirrels should last only as long as the woodpecker population is small and vulnerable to sudden extirpation.

ACKNOWLEDGMENTS

We thank J. R. Walters, R. G. Hooper, F. C. James, J. D. Ligon, S. C. Loeb, B. Parresol, and J. F. Taulman for constructive comments on an early draft of the manuscript. Partial funding was provided by a Challenge Cost Share Agreement (#19-90-008) with the Resource Protection Division, Texas Parks and Wildlife Dept.

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Wilson Bull., 108(4), 1996, pp. 712–727

HABITAT-USE PATTERNS IN COOPERATIVE AND NON-COOPERATIVE BREEDING BIRDS: TESTING PREDICTIONS WITH WESTERN SCRUB-JAYS

D. Brent Burt

Abstract.—I propose a method to test extensions of models concerning the maintenance of cooperative breeding systems that examines patterns of habitat use relative to the distribution of habitat components among territories. I analyzed habitat use and behavioral time budget data for a Texas population of the Western Scrub-Jay (*Aphelocoma californica*). As a non-cooperative population, one of two habitat-use patterns was expected: (1) specialist habitat-use patterns in an abundant, widespread habitat type, with little variation among territories in habitat composition or (2) generalist habitat-use patterns with the potential of significant variation in habitat composition among territories. These jays show a combination of habitat-use patterns supporting both predictions. The only resources that males utilize as a specialist, tall oak trees during sentinel behavior, are fairly widespread and would not be considered a limiting resource. In the remaining habitat categories, Texas populations of Western Scrub-Jays act as generalists, using the habitat in relation to its availability, even though variation in habitat composition among territories is considerable. Variation among individuals within a sex was observed but could not be explained using various demographic and ecological correlates. Additional detailed habitat use data when used in a comparative framework can aid determination of subtle ecological differences among populations of Western Scrub-Jays and allow closer examination of intrinsic and extrinsic ecological models concerning the evolution and maintenance of cooperative breeding systems in this group. *Received 27 Aug 1995, accepted 8 April 1996.*

Habitat use and the concept of ecological constraints have played a major role in the development of theories concerning evolution and maintenance of cooperative breeding in birds (Brown 1987, Koenig et al. 1992). Specifically, ecological constraints may serve as both intrinsic and extrinsic reasons for delayed dispersal, setting the stage for the helping behavior seen in cooperative breeding systems. Comparative studies of the genus *Aphelocoma* have been particularly instructive in testing the role ecological constraints play in the evolution of social systems because the genus exhibits extensive geographic variation in social systems and habitat use (Brown 1974, Fitzpatrick and Woolfenden 1986, Peterson and Burt 1992). The success of the comparative method rests on an even and complete sampling of taxa in the study group. To that end, this study documents the habitat use patterns of a non-cooperative population of Western Scrub-Jays (*A. californica,* see American Ornithologists' Union 1995), in central Texas.

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Using behavioral time-budget data, it is possible to test whether each major habitat component is used relative to its availability for each major behavioral category (i.e., individuals act as generalists) or whether certain behaviors are more likely to occur in specific habitats (i.e., individuals act as specialists). When behavioral-habitat specialization patterns are seen, we can then study in more detail the importance and distribution of this target of specialization and see if it is possibly a limiting resource critical in the determination of habitat quality. This study examines habitat composition of territories and habitat use patterns and determines (1) the generalist/specialist habitat use status of this population, (2) the availability and distribution of different habitat components and the presence of potentially limiting resources, and 3) how specific behaviors are related to each habitat component. As a non-cooperative population (Burt 1992), one of two habitat use patterns is expected (see discussion). First, the population may show specialist habitat use patterns, but only if in an abundant, widespread habitat type with little change in habitat composition among territories. Alternatively, the population may show generalist habitat-use patterns with significant variation in habitat composition among territories with individuals using each habitat component in relation to its availability. In the latter case no target of specialization is expected.

STUDY AREA AND METHODS

I conducted this study in oak-juniper woodland in Kerrville-Schreiner State Park, Kerrville, central Texas. The park's dominant woody vegetation was Texas live oak (*Quercus virginiana fusiformis*), Texas red oak (*Q. shumardii texana*), and Ashe Juniper (*Juniperus ashei*) (Miller and Lamb 1985). I partitioned the study area into 231 quadrats, 33.3 m^2 in area. In each quadrat, I characterized the woody vegetation composition in two ways: biodiversity or structural diversity. I characterized biodiversity into four categories by percentage of living oak (LO), dead oak (DO), living juniper (LJ), and dead juniper (DJ). I also characterized structural diversity into four categories by percentage of isolated living (IL), isolated dead (ID), dense living (DL), and dense dead (DD) patches of trees. I calculated percentages by actual counts of trees in each quadrat when possible and by visual estimates to the nearest five percent in dense vegetation. Because percentage estimates of vegetation are not comparable between quadrats of different vegetational density, I multiplied each percentage by the density of vegetation in that quadrat. The resulting number is the standardized, relative abundance of each vegetation type which can then be compared to the relative abundance all other quadrats. The density of vegetation in each quadrat was measured from aerial photographs using the transect method. Evenly spaced transect lines were drawn in each quadrat of the aerial photograph, and the length of line crossing trees was divided by total line length (Avery 1985; 87).

I used mist nets to capture 66 jays and marked them with U.S. Fish and Wildlife Service leg bands and a unique combination of three colored metal bands. I aged adult jays as first-year birds or older based on plumage characters (Pitelka 1945). During the breeding season, jays were sexed by presence or absence of a brood patch. Individuals captured at other times

were sexed by behaviors and vocalizations. I determined territory boundaries by observing territorial conflicts and home range use and then mapped each on aerial photographs. I calculated vegetational composition for each territory each year by averaging numbers of each vegetation type for each quadrat in each territory.

I collected focal sampling data from 7 June to 6 July 1989 on four breeding pairs and from 14 June to 29 June 1990 on five breeding pairs. All behaviors were recorded to the nearest second in 15-min sampling sessions or until the bird was lost from sight. Sessions where the bird's behavior was affected by observer presence were excluded from analysis. I categorized behaviors as sentinel, foraging, inactive/preening, territorial, or other (begging, caching, sunning, etc.). Sentinel behavior included any behavior engaged in when an individual was perched on a tall exposed branch, and its designation overrides concurrent behaviors such as preening or territorial calling. I recorded the following data in addition to behavior: general weather, time of day, substrate used (same vegetation categories as in quadrat sampling), location in territory, the presence/absence of other jays, and food type eaten (when possible). I collected data from 07:00 to 20:00 CST using a stop watch, tape recorder, and 10 × 40 binoculars. An effort was made to observe marked individuals for equal amounts of time, evenly spaced throughout the time of day and season. Individuals to be sampled were predetermined each day to avoid observer biases that could result in simply observing the first bird seen.

For each individual in each year, I calculated percentages of time spent in each behavior in each main vegetation type listed above. These observed values were then compared to the availability of this habitat in the individual's territory. Time spent on substrates other than woody vegetation (i.e., buildings, fences, the ground) was excluded from analyses. Data were checked for normality (Lilliefors' test) and homogeneity of variances (F-max test), and then either paired comparison t-tests, t'-tests (comparisons of groups with unequal variance), Mann-Whitney U tests, or two-way ANOVAs were used to examine statistical significance where appropriate (Sokal and Rohlf 1981, Neave and Worthington 1988). Percentage data were arcsine transformed for parametric tests. All tests are two-tailed. Bonferroni's correction is applied to probability values for multiple tests that share portions of the data set. Statistical values and associated probabilities are given for all comparisons, but because of the conservative nature of these tests when dealing with small sample sizes, trends for values approaching significance are considered for potential biological importance.

Methodological limitations.—Two approaches to studying habitat use and behavioral time budgets were considered for this study. One approach is to follow many individuals and have fewer sampling sessions per individual. This method might reduce the variance among individuals for each behavioral category, but it is impractical if behaviors vary temporally (i.e., within a day, month, season). This variation would require equal sampling through time for all individuals. Behavioral patterns show temporal variation in the Florida Scrub-Jay (*A. coerulescens*; DeGange 1976). The approach in this study was to follow fewer individuals for more sampling periods, more or less regularly spaced through time (day and season). The difficulties with this approach are limited sample sizes for statistical tests and the potential for large among-individual variation.

RESULTS

General habitat use.—This first analysis examines whether each sex uses each habitat component relative to its availability when all behaviors are examined together. Bonferroni's corrected probabilities needed for statistical significance in this test are $P = 0.05/2$, or $P = 0.025$. When considering biodiversity habitat categories (Fig. 1A), males used living

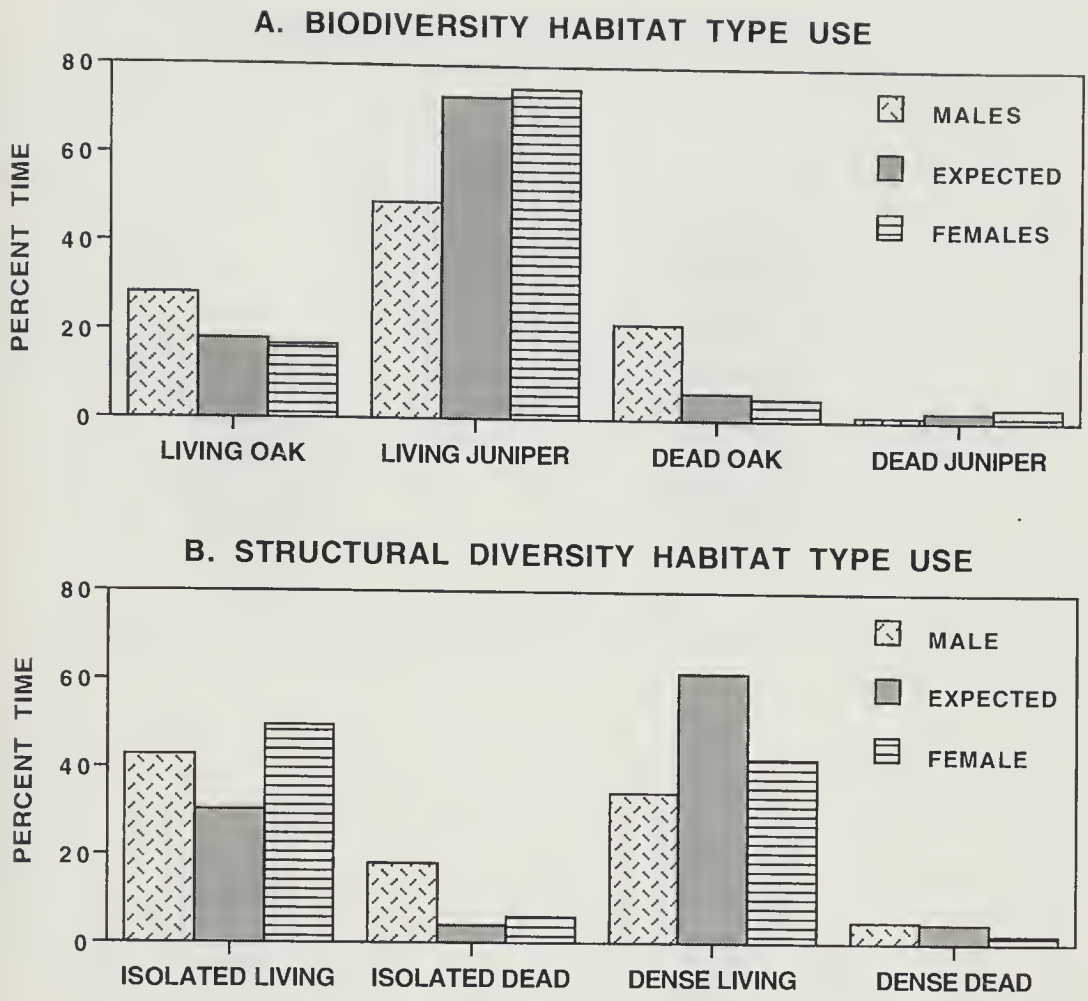

FIG. 1. Observed and expected time percentages birds spent in each biodiversity (A) and structural diversity (B) habitat category in 1989.

juniper (LJ) significantly less than expected on the basis of its availability in 1989 (t = 7.7, P = 0.0045), and possibly in 1990 (t = 3.03, P = 0.039), but used living oak (LO), dead juniper (DJ), and dead oak (DO) in proportion to their availability (1989: LO, t = 1.06, P = 0.37; DJ, t = 2.0, P = 0.14; DO, t = 2.8, P = 0.068 df = 3. 1990: LO, t = 1.4, P = 0.22; DJ, t' = 1.2, P = 0.29; DO, t' = 1.8, P = 0.14), although dead oak approaches a statistically significant increase in use for 1989. Females use each habitat in proportion to its availability (1989: LJ, t = 0.45, P = 0.68; LO, t = 0.58, P = 0.60; DJ, t = 0.0086, P = 0.94; DO, t = 0.66, P = 0.56. 1990: LJ, t = 0.73, P = 0.50; LO, t = 0.0084, P = 0.99; DJ, t' = 1.3, P = 0.27, DO, t' = 0.19, P = 0.86).

Relative to woody vegetation structural diversity, males in 1989 used isolated living (IL) habitat significantly more than expected (t = 22.9, P = 0.0002) and dense living (DL) significantly less than expected (t =

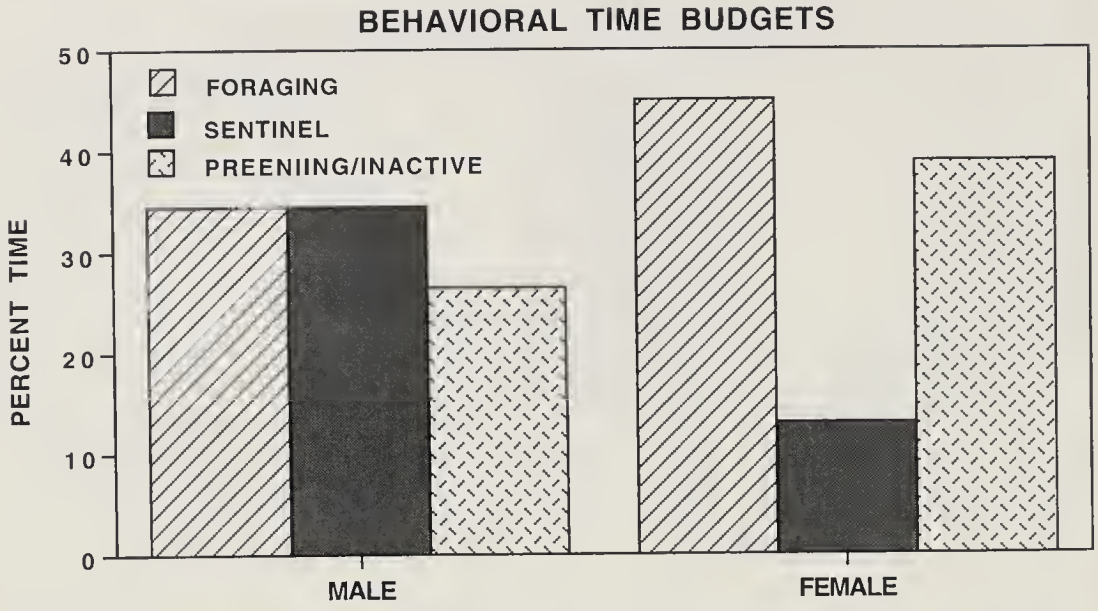

FIG. 2. Percentages of time spent in the three main behavioral categories in 1989.

5.5, $P = 0.012$) (Fig. 1B). Females had a similar pattern for 1989 (IL, $t = 5.2$, $P = 0.014$; DL, $t = 2.8$, $P = 0.067$) although this pattern was not statistically significant. Neither use of isolated living nor dense living habitats were different from expected in 1990 for males (IL, $U = 14.5$, $P > 0.2$; DL, $U = 16$, $P > 0.2$) or females (IL, $U = 16.5$, $P > 0.2$; DL, $U = 12.5$, $P > 0.2$). Use of isolated dead (ID) habitat was greater than expected by males in both years (1989, $t = 2.45$, $P = 0.092$; 1990, $t = 2.45$, $P = 0.070$) but not by females in either year (1989, $t = 0.72$, $P = 0.52$; 1990, $t = 0.61$, $P = 0.57$). In each year, use of dense dead (DD) habitat did not differ from expected for either males (1989, $t = 0.25$, $P = 0.82$; 1990, $t' = 0.98$, $P = 0.38$) or females (1989, $t' = 1.95$, $P = 0.15$; 1990 $t' = 1.15$, $P = 0.31$).

Behavioral time budget.—In this analysis, the pair studied only in 1990 was excluded to create a balanced two-way ANOVA for comparisons of each of the three main behavioral categories (Fig. 2). The ANOVA tests differences between sexes and years for each behavior. For the preening/inactive category no differences existed between sexes ($F_{1,12} = 0.11$, $P > 0.50$), or between years ($F_{1,12} = 0.044$, $P > 0.75$), and no interaction effect existed ($F_{1,12} = 0.38$, $P > 0.50$). Males spent more time in sentinel behavior than did females ($F_{1,12} = 8.6$, $P = 0.012$) but no significant difference existed between years ($F_{1,12} = 1.6$, $P = 0.23$) nor was an interaction effect seen ($F_{1,12} = 0.63$, $P > 0.25$). Foraging data had significant heteroscidacity and therefore a test of equality of means (Games and Howell method, Sokal and Rohlf 1981) was performed in lieu of a two-way ANOVA. Unplanned comparisons among all means showed no

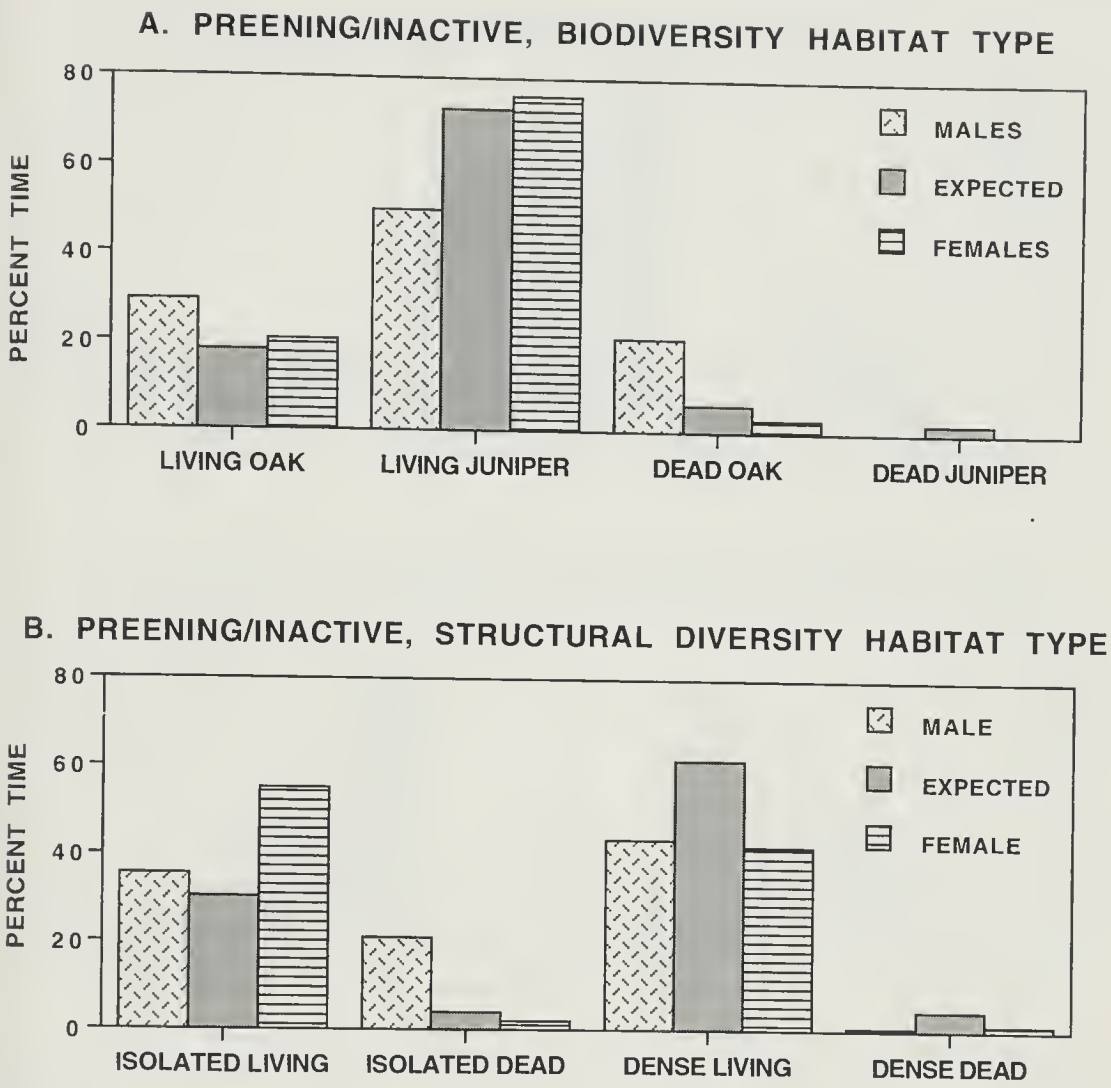

FIG. 3. Observed and expected percentages of time birds spent in each biodiversity (A) and structural diversity (B) habitat category in 1989 while preening/inactive.

significant differences in time spent foraging between either sexes or years at $P \leq 0.05$.

Behavioral differences in habitat use.—The next series of analyses examine whether each sex uses each habitat component relative to its availability during each specific behavior. Bonferroni's corrected probabilities needed for statistical significance in these tests are $P = 0.05/6$, or $P = 0.0083$. For both years, neither males nor females spent more or less time than expected preening or inactive in any category of habitat classified by either biodiversity or structural diversity (Fig. 3). Four values do, however, approach $P = 0.05$ in the biodiversity categories (male LJ, 1989, $t = 2.55$, $P = 0.084$, 1990, $t = 2.05$, $P = 0.11$; male and female DJ 1989, $U = 16$, $P = 0.05$) and four values approach significance for the

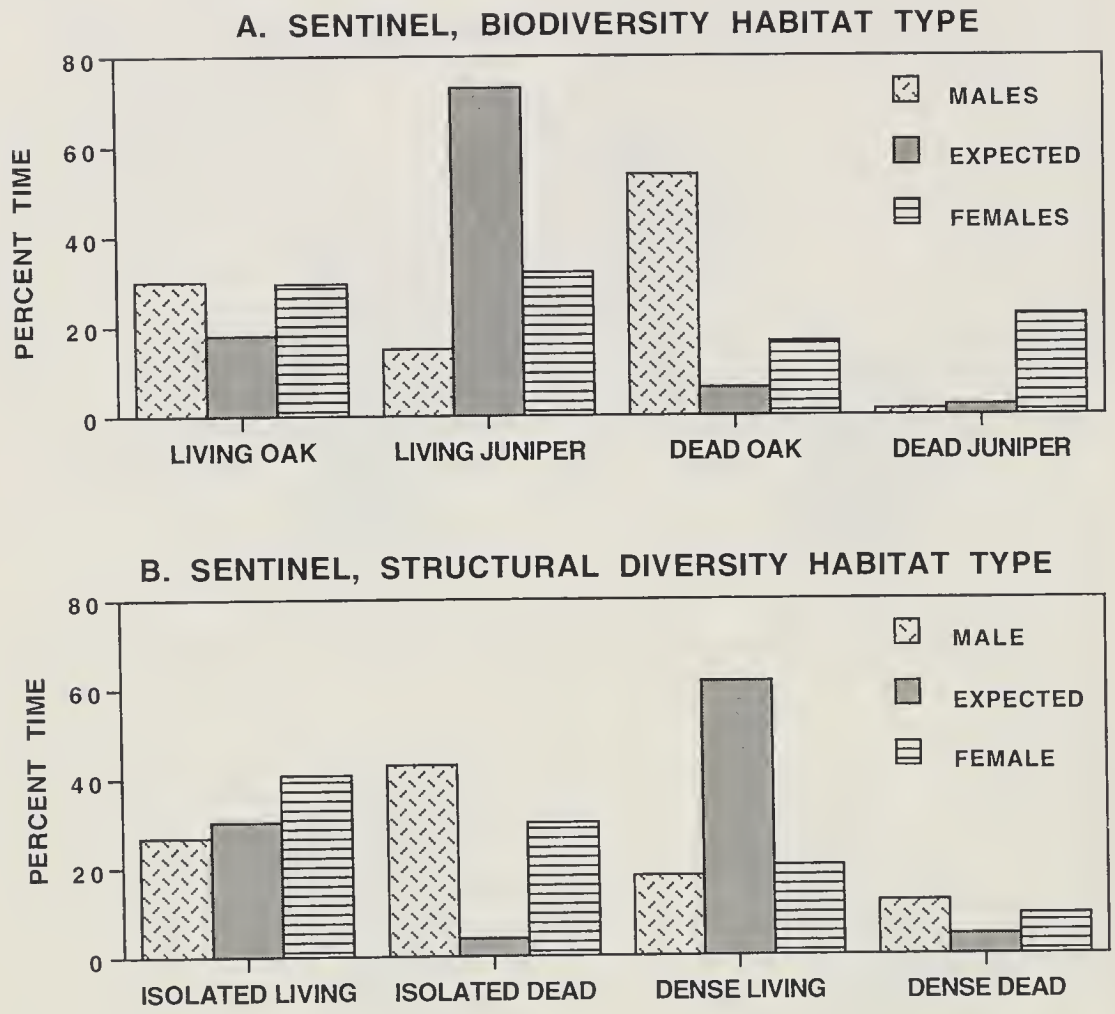

FIG. 4. Observed and expected percentages of time birds spent in each biodiversity (A) and structural diversity (B) habitat category in 1989 while sentinel.

structural diversity categories (male DL 1990, $t = 2.98$, $P = 0.041$; female IL 1989, $t = 3.14$, $P = 0.052$; male and female DD 1989, $t = 3.46$, $P = 0.04$).

For sentinel time in biodiversity categorized habitats (Fig. 4A), males spent less time in living juniper in 1989 ($t = 6.28$, $P = 0.0082$) and possibly in 1990 ($U = 25$, $P = 0.01$). Females also may have spent less sentinel time in living juniper in both years (1989, $U = 16$, $P = 0.05$; 1990, $U = 25$, $P = 0.01$). A pattern of more than expected use of dead oak during sentinel behavior is suggested, but only the value for males in 1990 is significant ($t' = 7.611$, $P = 0.0016$). In all other categories and years, observed percentages do not differ from those expected based on habitat availability. Sentinel time in structural diversity categories (Fig. 4B) indicates males, and possibly females, used isolated living trees less than expected in 1990 (male, $t = 4.62$, $P = 0.01$; female, $U = 25$, $P =$

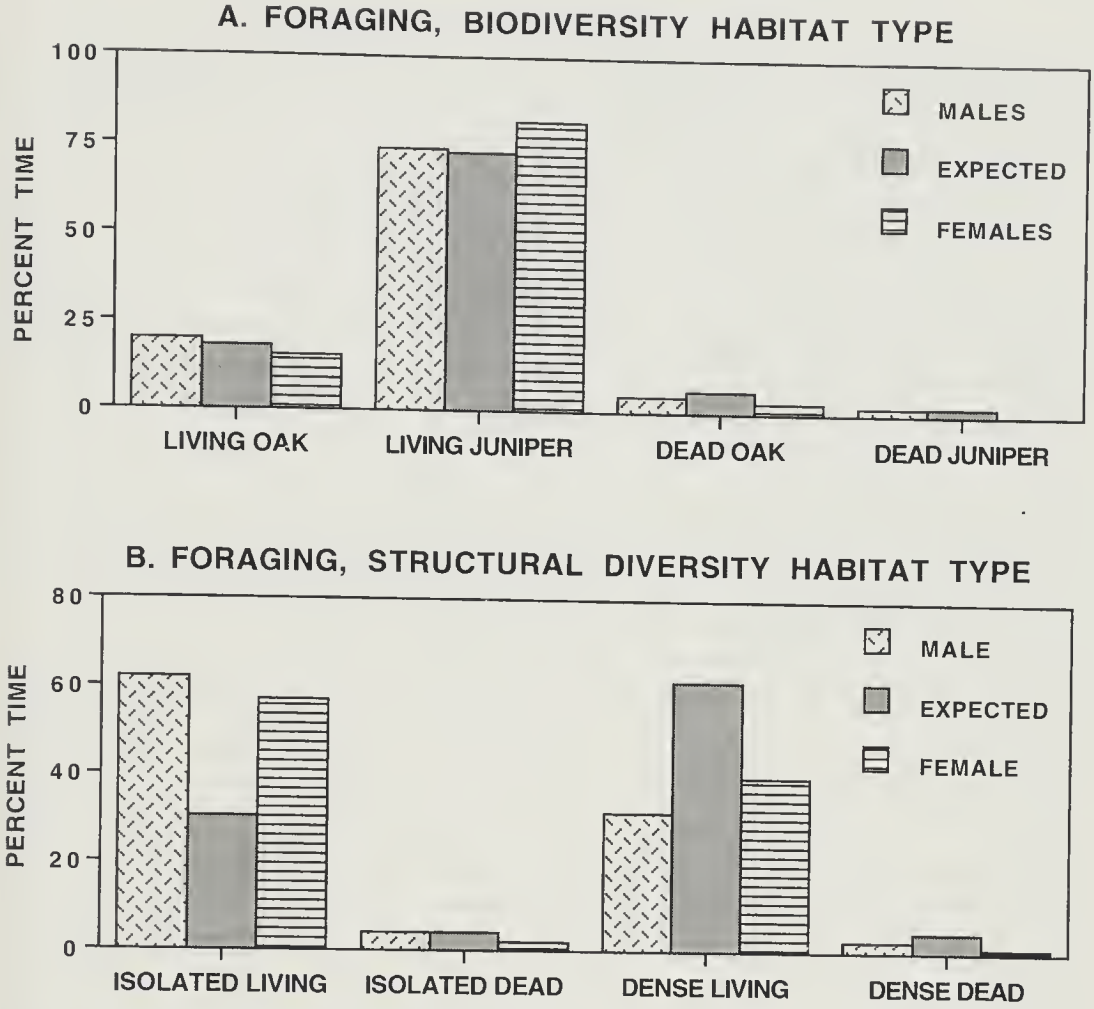

FIG. 5. Observed and expected percentages of time birds spent in each biodiversity (A) and structural diversity (B) habitat category in 1989 while foraging.

0.01) but not 1989. Increased use of isolated dead vegetation for both sexes in each year is suggested by the data, but values are not significant. All other comparisons for sentinel time in structural diversity categories do not differ from expected.

Foraging time does not differ from expected for either sex in either year in any biodiversity categories of vegetation (Fig. 5A). Five values approach significance in some of the rarer habitat categories (male and female DO 1990, $t' = 4.50$, $P = 0.011$ and $t = 3.59$, $P = 0.023$; female DO 1989, $t = 2.72$, $P = 0.073$; male DJ 1990, $U = 21$, $P = 0.1$; female DJ 1989, $U = 16$, $P = 0.05$). Foraging time in structural diversity categories of vegetation shows males, and possibly females, used isolated living vegetation more than expected in 1989 (male, $t = 7.78$, $P = 0.0044$; female, $t = 2.43$, $P = 0.094$) but not in 1990 (Fig. 5B). Males, and possibly females, also used the fairly rare category of isolated dead trees

less than expected in 1990 (male, $t = 5.63$, $P = 0.0049$; female, $t = 2.79$, $P = 0.049$) but not in 1989. Three other values approach significance in rare habitats (male and female DD 1990, $t = 3.55$, $P = 0.024$ and $t = 2.77$, $P = 0.05$; female DD 1989, $t = 5.074$, $P = 0.015$).

DISCUSSION

Habitat use and the concept of ecological constraints are central to many theories concerning the evolution and maintenance of cooperative breeding in birds. Specialization in habitat use in long-lived birds and the resulting potential to saturate this habitat is central to both the habitat saturation and marginal habitat models. The habitat saturation model states that suitable breeding habitat slots become filled, forcing young individuals to delay dispersal (Selander 1964, Brown 1974). The marginal habitat model builds on this concept by adding an additional constraint, namely scarcity of habitats of marginal quality. Scarcity of marginal habitats reduces the possibility of individuals dispersing and roaming as nonbreeding floaters (Verbeek 1973, Koenig and Pitelka 1981, Emlen 1982, Woolfenden and Fitzpatrick 1984, Fitzpatrick and Woolfenden 1986). One prediction of the marginal habitat model is a high proportion of territories of high-quality habitat relative to those of marginal quality in cooperative breeding populations. As an alternative to these extrinsic constraint models, the benefits-of-philopatry (BOP) model stresses the importance of intrapopulational variation in territory quality and is not dependent on complete saturation of either breeding or marginal/floating habitats but is instead based upon the intrinsic decision making processes of young birds regarding their dispersal options relative to the quality of their natal territory (Stacey and Ligon 1987, 1991). According to this model, individuals born in high quality natal territories choose to delay dispersal and remain at home, thereby increasing their chances of inheriting the natal territory or occupying another nearby territory of equal quality. These individuals also may avoid increased chances of mortality associated with breeding or floating in lower quality habitats. Koenig et al. (1992) introduced an elegant, more inclusive model, which more formally distinguishes between extrinsic and intrinsic factors influencing an individual's decision on whether to delay natal dispersal. This delayed dispersal threshold model identifies five parameters that are many times jointly involved in the probability of an individual delaying dispersal. A complete explanation of this model is not possible here, however, in regard to this paper, one of its parameters is the distribution of territory quality as modeled in either the marginal habitat or BOP models.

An extension of current models.—I believe the logic outlined in each of these models can be extended to predict specific habitat use patterns

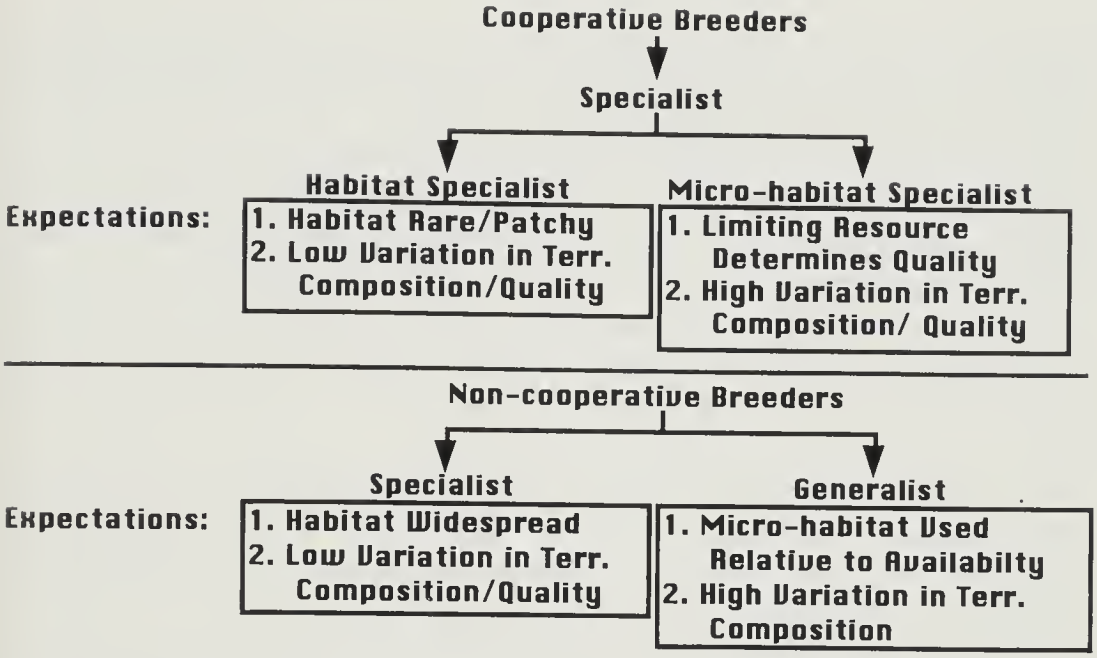

FIG. 6. Model of habitat-use expectations for cooperative and non-cooperative breeding populations.

for cooperative and non-cooperative breeding populations (see Fig. 6). One might expect cooperative populations to show restricted, habitat specialist patterns of habitat use in one of two ways. First, a population may show a strict requirement to live in a habitat characterized by a certain vegetation assemblage. This habitat-use inflexibility would lead to demographic conditions favoring the evolution of cooperative breeding only if the habitat in question is either rare in comparison to other assemblages in the same geographic region or is very patchily distributed. With such broad habitat-use specificity, variation among usable territories in habitat composition and quality may be small. In extreme cases, all habitat patches in an area are either acceptable or unacceptable for breeding or floating, with no intermediaries. These predictions fit the habitat saturation model and, depending on the degree of habitat specificity (i.e., does marginal habitat even exist for the species), the marginal habitat model. The second habitat-specialist pattern to be expected from a cooperative population is the required use of a *particular* aspect of the habitat, a target of specialization, that serves as a limiting resource while other aspects of habitat composition have reduced importance and may vary independently among territories. In this case, general habitat composition may vary greatly but be of little importance. The presence of the limiting resource is the crucial feature of successful breeding in this situation and is the currency by which territory quality is measured. Examples of such targets

of specialization in cooperative species include cavities for both Green Woodhoopoe (*Phoeniculus purpureus,* Ligon and Ligon 1988) and Red-cockaded Woodpecker (*Picoides borealis,* Kulhavy et al. 1995) for roosting and nesting, and granary trees for acorn storage by Acorn Woodpeckers (*Melanerpes formicivorus,* Koenig and Mumme 1987). If territory quality varies greatly and is tightly correlated with reproductive success, as predicted by the BOP model, a cooperative breeding system may evolve as a queue of non-dispersing individuals builds to fill the small number of high quality breeding territories. In this latter case, it is necessary to demonstrate that individuals utilize the limiting resource disproportionately to its availability in the territory.

Non-cooperative populations also would be expected to show one of two habitat-use patterns (Fig. 6). First, non-cooperative populations also may show specialist habitat-use patterns but only in a super-abundant, widespread habitat type. In this case, territory composition should not change much among territories. Alternatively, the population may show generalist habitat-use patterns with significant variation in habitat composition among territories. In the latter case, it is expected that individuals use each habitat component in relation to its availability and no target of specialization is expected.

Measuring territory quality has proven difficult and is flawed in many studies because reproductive success is used as the primary currency which fails to distinguish between habitat quality and the quality of individuals (Koenig et al. 1992). However, I believe documentation of habitat-use patterns allows closer examination of the mechanisms leading to changes in breeding systems. This approach must first classify populations as habitat specialist/generalist relative to other populations based on knowledge of the distribution of each major habitat component across territories and detailed habitat-use patterns of these major components. Then, given the two predictions concerning patterns of habitat-use for both cooperative and non-cooperative populations and information on population variation in breeding systems, we can examine the models concerning the ecological bases of cooperative breeding systems more closely.

Behavioral patterns in biodiversity habitat categories.—Texas Western Scrub-Jays use the biodiversity categories of woody vegetation as generalists with one exception: males use living juniper less than expected with the excess time transferred to dead and living oaks (Fig. 1A). The behavioral explanation for this deviation is the large fraction of time males engage in sentinel behavior and the relatively poor visibility attributes of (usually short) living juniper and the good visibility attributes of (usually tall) oak trees. Females also use these habitat categories in this

pattern, but because so little of their time is spent in sentinel behavior, deviations from general use of this habitat type are not as large (Figs. 2, 4A). Males also may have used living juniper while preening/inactive less than expected (Fig. 3A). The habitat in which this behavior occurs may be influenced by the habitat in which the behavior preceding it occurred. Individuals may simply preen wherever they find themselves and, in general, males spent little time in living juniper. Values approaching significance in differential use of several of the rarer biodiversity categories should not be given much weight because of the potential for sampling error in categories where behaviors appear also to be rare (e.g., foraging in DO and DJ, Fig. 5A).

Behavioral patterns in structural diversity categories.—Observed values deviated from expected values in more structural diversity categories than in biodiversity categories (Fig. 1B). As noted above, males and females used isolated living vegetation more than expected at the expense of dense living trees in 1989 but not in 1990. Similarly males, and possibly females, used isolated living vegetation while foraging more than expected in 1989 but not 1990 (Fig. 5B). This pattern could have been due to a food resource shift between years; however, no data exist to test this possibility. The two most frequently captured prey items were large katydids (probably *Microcentrum* sp.) and walking sticks (probably *Megaphasma* sp.), but their distribution among the different habitat categories is unknown. Deviations from expected in habitat use of preening/inactive behavior seem to mirror those of foraging behavior in females but not in males (Fig. 3B). Again, if individuals preen wherever they find themselves, foraging would influence where the preening/inactive behavior occurred in females more than in males, because females spent a large fraction of their time foraging, while males were influenced by both foraging and sentinel behaviors (Fig. 2).

Males also may have used isolated dead vegetation more than expected in both years (Fig. 1B). Both sexes increased use of this habitat for sentinel behavior (Fig. 4B); however, not all deviations from expected are close to statistical significance. Much of the isolated dead habitat is equivalent to the dead oak category of the biodiversity categorization, and a functional relationship of isolated dead trees to sentinel behavior probably exists. Both males and females also used isolated living vegetation for sentinel behavior less than expected in 1990 but not 1989. This difference is not observed in general habitat use (Fig. 1B), and reasons for this deviation while in sentinel behavior are not apparent.

Habitat use patterns of other scrub-jay populations.—Peterson and Vargas (1992) provide a thorough analysis of the diversity of habitat types used by birds in the scrub-jay species complex. Scrub-jays use a wide

range of habitats including: oak, juniper, pinyon and desert woodlands; riparian brush; oak-palmetto scrub; pine-oak, alpine pine-spruce, tropical thorn forests; and mangrove swamps. This level of variation in habitat use is that which occurs *across populations.* Levels of variation in habitat use *within populations* is highly population specific. Florida, coastal California, and Great Basin populations are very habitat specific. This specificity was hypothesized to be related to the importance of either acorns or pinyon seeds in the diet of these populations. Baja California and southern Mexico populations are more general in habitat use, and these habitats frequently have no obvious replacements for acorns or pinyon seeds. Koenig et al. (1992) discuss the importance of mast production relative to differences in social systems in scrub-jays. In the non-cooperative California population of Western Scrub-Jays, years of poor acorn abundance result in increased reproductive failure, adult mortality and territory abandonment. Oaks are distributed in patches in California and floaters typically move freely among breeding territories in search of areas of high acorn abundance (Carmen 1988). Concerning the Florida Scrub-Jay, mast production is more stable in Florida and this predictable, evenly distributed, resource is easily defended and floaters are not tolerated in breeding territories. Koenig et al. (1992) also speculate that differences in mast production partially explains differences in jay use of the optimal, recently burned oak patches and unoccupied, dense, unburned patches of oaks.

Presence of other jay species affects range of habitat use in Florida (Blue Jays, [*Cyanocitta cristata*]), central California (Steller's Jays [*C. stelleri*]), and New Mexico/Arizona (Gray-breasted Jays) but does not limit use in southern Mexico (Magpie-Jays [*Calocitta* spp.]). However, the diversity of habitats utilized by Scrub-Jays in Baja California cannot be solely explained by the absence of other jay species because this population uses habitats that are not used on the mainland by any jay species (Peterson and Vargas 1992).

Habitat use and predictions of models for the Texas population.—In most habitat-use categories examined in this study, the central Texas population of Western Scrub-Jays appears to use its habitat as a generalist. The only clear exception to this statement is the apparent specialization by males in using oak, particularly isolated snags, for sentinel behaviors. As a non-cooperative population, one of two habitat-use patterns was expected (1) specialist habitat-use patterns in an abundant, widespread habitat type, with little variation among territories in habitat composition (matching the habitat saturation or marginal habitat models), or (2) generalist habitat-use patterns with the potential of significant variation in habitat composition among territories (as predicted under the BOP

model). Texas Western Scrub-Jays show an interesting combination of habitat-use patterns supporting both predictions. The only resources that males utilize as a specialist, oak trees during sentinel behavior, are fairly widespread and would not be considered a limiting resource. In the remaining habitat categories Texas Western Scrub-Jays act as generalists, using the habitat in relation to its availability, even though variation in habitat composition among territories is considerable. Mast production, an important resource to many jay populations, was not measured in this study because of the season in which data were collected.

Areas in need of future research.—Comparisons between cooperative and non-cooperative populations using more detailed habitat-use studies, when combined with demographic and phylogenetic information, will allow closer examination of the various models of the evolution and maintenance of cooperative breeding in birds. It is clear that habitat constraints are important in the Florida Scrub-Jay and examining habitat use in their relict scrub habitat may reveal why very dense, unburned scrub and other habitats are inadequate for maintaining populations (Woolfenden and Fitzpatrick 1984). This subject is the focus of a detailed habitat-use study currently underway (R. Curry, pers. commun.) This type of detailed study also would be most valuable for examining correlations between ecological constraints and cooperative breeding in the southern Mexico population of the Western Scrub-Jay. This population appears to use a wide range of habitat types which do not appear saturated (Burt and Peterson 1993). A detailed habitat-use study might identify specific microhabitats that limit where successful territories can be maintained. These microhabitats may be found to exist within several of the more broadly defined habitat types. As shown in this study, habitat-use patterns can be used to test predictions concerning the role ecological constraints play in determination of individual dispersal patterns and, potentially, the evolution of breeding systems.

ACKNOWLEDGMENTS

I thank the Texas Dept. of Fish and Wildlife for permission to conduct this study in the Kerrville State Park. Special thanks go to Tim Hufstedler and the rest of the park staff for their cooperation and assistance. Terry Maxwell allowed me to apply for a banding subpermit under his permit number. Financial assistance was provided by grants from the American Museum of Natural History (Chapman Grant), Univ. of Kansas Museum of Natural History (Panorama Society grants), Texas Ornithological Society, the Univ. of Kansas Dept. of Systematics and Ecology, and the Univ. of Arizona Research Training Group for the Analysis of Biological Diversification. Richard Johnston and Phil Humphrey were particularly helpful in my attempts to find financial support. My committee members, Ken Armitage, Mike Gaines, Doug Siegel-Causey, and Richard Johnston (Chair) provided guidance and careful consideration of early drafts of this manuscript as did Robert Curry, Ronald Mumme, Daniel Papaj, and Glen Woolfenden, members of the Nathaniel Goss Society

(Univ. of Kansas), and two anonymous reviewers. Persons who were generous with their time in sharing ideas and/or field work include Tristan Davis, Sue Fairbanks, John Koprowski, Brad Livezey, Terry Maxwell, and Mike Stokes. I also thank Kim Burt and my family for their continued support.

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Wilson Bull., 108(4), 1996, pp. 728–739

NUTRITIONAL VALUE OF WINTER FOODS FOR WHOOPING CRANES

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ABSTRACT.—We measured metabolizable energy and digestibility of Whooping Crane (*Grus americana*) winter foods (blue crab [*Callinectes sapidus*]), common *Rangia* clam (*Rangia cuneata*), wolfberry fruit (*Lycium carolinianum* [wolfberry]), and live oak acorn (*Quercus virginiana* [acorn])] with feeding trials to captive-reared Whooping Cranes. Apparent metabolizable energy coefficients (expressed as %) were for crab (34.1), *Rangia* clam (75.0), wolfberry (44.8), and acorn (43.2). Digestion coefficients for protein were lower for plant foods (48.9 and 53.4) than for animal foods (69.4 and 75.2). Digestion coefficients for total lipid differed among foods: highest and lowest lipid digestibility was for acorn (87.2) and wolfberry (60.0), respectively. We also determined total energy and percent protein and lipid of the four foods and stout razor clam (*Tagelus plebeius*); gross energy was 2–5× higher for acorn and wolfberry on a dry-weight basis than for blue crab and stout razor clam. Crude protein was 2–3× higher for blue crab than for wolfberry and stout razor clam. Wolfberry ranked the highest of five foods for metabolic energy and total lipid nutrient availability per kg of food ingested, and blue crab ranked highest for crude protein availability. *Received 1 December 1995, accepted 10 April 1996.*

Investigators have documented foods eaten by Whooping Cranes on their Texas Coastal wintering ground (Aransas National Wildlife Refuge [ANWR]). They have determined that Whooping Cranes rely on blue crabs (*Callinectes sapidus*), stout razor clams (*Tagelus plebeius*), wolfberries (*Lycium carolinianum*), and acorns (*Quercus virginiana*) for their energy and nutrient needs (Stevenson and Griffith 1946; Allen 1952, 1954; Shields and Benham 1969; Uhler and Locke 1970; Blankinship 1976; Hunt and Slack 1987, 1989). In order to determine if winter food resources are adequate, managers should understand metabolizable energies, nutrient digestibilities, and nutritional values of these foods. Our objectives were to determine (1) metabolizable energy and nutrient digestibility coefficients for winter Whooping Crane foods, by feeding them to captive Whooping Cranes, and (2) the energy and nutritional content of these foods.

METHODS

We conducted feeding trials with captive-reared Whooping Cranes in spring 1994 at Patuxent Environmental Science Center (PESC), Laurel, Maryland. Because of the endan-

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gered status of Whooping Cranes (U.S. Fish and Wildl. Serv. 1994), we used captive-reared birds in our digestibility studies. Cranes were raised on pelleted diets, could not be induced to eat whole foods voluntarily, and unacceptable risks were associated with forced feeding. The amount of wild foods we were able to collect influenced the amount and length of time food was fed to individual birds. The amount of time captive birds could be maintained under experimental conditions was also limited because we were concerned about behavioral problems and risk of injury. Therefore, treatment diets were mixed with control diets and fed to captive Whooping Cranes during short time periods. Wild foods were provided in pelleted feeds at a 30% level of substitution because of concerns that captive cranes might be adversely affected by eating feeds with higher levels of wild foods and might reduce feed consumption at levels higher than 30% (Muztar et al. 1977). Thus, we were unable to conduct validation trials using 100% wild foods.

We housed four subadult (1-yr-old) and one adult (3-yr-old) Whooping Cranes in adjacent 3.4 × 2.7 × 3.1-m indoor pens at the PESC during feeding trials from 2 March to 27 April 1994. Connected to each indoor pen was a 9.1 × 2.9 × 2.9-m outdoor runway. Each indoor pen was equipped with a gravity feeder, water bucket, and a bowl for granite grit. Floors were covered with smooth rubber matting to collect excreta. Cranes were allowed to move between indoor and outdoor runways on days when they were not fed study diets and were housed indoors at night. Indoor photoperiod was maintained at 10.5D:13.5L, and indoor temperature ranged from 13°C to 25°C. Cranes were weighed to the nearest 100 g with a spring scale (1) when first moved to the Propagation Building, (2) six days after the initial move, and (3) when the study was completed. Daily at 06:00, we fed 1000 g each of blue crab, *Rangia* clam, acorn, and reference feeds and 400 g of wolfberry feed.

We collected acorns, blue crabs, wolfberries, and *Rangia* clams from Whooping Crane foraging areas on the ANWR Blackjack Peninsula and Matagorda Island, Texas, and adjacent coastal areas between 8 October 1993 and 17 February 1994 (Labuda and Butts 1979, Stehn 1994b, U.S. Fish and Wildl. Serv. 1994). Acorns were also collected at College Station, Texas, to supplement acorns collected at the ANWR. Whooping Cranes prefer stout razor clams (Blankinship 1976), but we could not collect sufficient numbers; instead, we collected the less preferred *Rangia* clam for our feeding trials. Foods were stored at −20°C until they were dried at 55°C for 24–36 h and ground in a Wiley or Hammer mill to pass through a 20-mesh screen. Study diets were prepared by combining 30% dry weight of blue crab, *Rangia* clam, wolfberry, or acorn with 70% commercial crane breeder feed. We added bentonite (0.5%) to each diet as a hardening agent and an inert tracer, chromic oxide (0.5%), to determine metabolizable energy and nutrient digestibility coefficients (Karasov 1990). Moistened diets were mixed in a Hobart food mixer, formed into pellets (0.48-cm diameter) using a Hobart food processor, and air dried and stored in plastic bags at 5°C until feeding.

Apparent metabolizable energy coefficients (MEC*) for test feeds were determined using the equation of Karasov (1990): $MEC^* = [GE_i - (\%T_i/\%T_e)GE_e]/GE_e$; where GE_i and GE_e equal, respectively, the gross energy content (cal·g^{-1} dry mass) of feed (intake) and excreta, and $\%T_i$ and $\%T_e$ equal, respectively, the percent of chromic oxide tracer in feed and excreta. Apparent digestible energy coefficients for test feeds (DEC*) were determined by subtracting percent gross energy of uric acid in excreta (% uric acid multiplied by 2730 cal·g^{-1}) (Lide 1994) from total gross energy of excreta (GE_e) and substituting energy excreta (minus uric acid energy) into the equation for MEC*. Individual MEC*s for test ingredients were determined by equation 2: $MEC^*_i = {}^{100}/_{30} \times (MEC^*_f - [0.7 \times MEC^*_r])$; where MEC^*_i equals the MEC* for the test ingredient, MEC^*_f equal the MEC* for the test feed (feed with test ingredient added), and MEC^*_r equal the MEC* for the reference feed (indicator-marked crane breeder feed) (Wilson and Poe 1985). Apparent digestible energy coefficients for test ingredients (DEC^*_i) were determined by substituting energy excreta (minus uric acid energy)

into the equation for MEC^*_i, where DEC^*_f equal the DEC* for the test feed and DEC^*_r equal the DEC* for the reference feed: $DEC^*_i = (100/30) \times [DEC^*_f - (0.7 \times DEC^*_r)]$.

Apparent dry matter, crude protein, and total lipid digestibility coefficients for test feeds and reference feed (ADC_f) were determined using an index equation by Lloyd et al. (1978):

$$ADC_f = 100 - \left[100 \times \frac{(\%\ \text{Indicator in feed})}{\%\ \text{Indicator in feces}} \times \frac{(\%\ \text{Nutrient in feces})}{\%\ \text{Nutrient in feed}}\right]$$

on the basis of the ratios of indicator in feed and feces and nutrient in feces and feed. Apparent digestibility coefficients for test ingredients (ADC_i) were determined by substituting apparent dry matter, crude protein, and total lipid digestibility coefficients for test feeds and reference feed into equation 2. Digestible protein for test feeds was determined after subtracting uric acid nitrogen in excreta from total Kjeldahl nitrogen in excreta (Rotter et al. 1989).

MEC*s for wild foods with low digestibilities have been shown to be low and in error for waterfowl fed mixed diets (Karasov 1990). However, Muztar et al. (1977) found that apparent dry matter digestibility and apparent metabolizable energy values were higher at the 30% level of substitution than at 10%, 20%, or 40% for alfalfa and five species of aquatic plants and that 30% substitution agreed most closely with regression methods to predict digestibility. Our model for determination of MEC* is based upon the assumption that relations between MEC* values are additive and that there are no synergisms or associative effects for MEC* and nutrient digestibilities due to mixing feed ingredients (Cho et al. 1982, Wilson and Poe 1985).

Diets were fed following a Latin Square design with five, four-day feeding trials. We fed cranes an unmarked breeder diet during a three-day rest period between trials to allow them to excrete all indicator-marked food. Whooping Cranes were held indoors during feeding trails except for four, 30–45-min periods starting at 06:00, 10:00, 14:00, and 18:00 when they were moved outdoors while we collected excreta from the rubber matting and cleaned floors. Fecal samples were collected separately for each bird and for each collection period from indoor pens; samples for each bird and collection period were pooled. Samples collected on days three and four of each feeding trial were used to estimate metabolizable energy and digestibility coefficients. We used change in indicator concentration on the first day indicator-marked diets were fed to evaluate rate of food passage (length of time unmarked feed was retained in the gut).

We collected samples of blue crabs, *Rangia* clams, wolfberries, acorns, and stout razor clams from six different sites on the ANWR (Stehn 1994b, U.S. Fish and Wildl. Serv. 1994). Each collection site was 1–10 ha depending on the relative density and distribution of foods collected, and one food type was collected. We collected nine samples of each food from points on transect lines located at random within each collection area. Sample collections of food items included (1) acorns—8–20 of varying sizes from ≥five plants from Dagger Point and (2) along East Shore Road to the west of Sundown Bay, (3) stout razor clams—10–20 individuals 3–4 cm long from Cedar Lake, Matagorda Island, (4) *Rangia* clams—8–10 individuals 3–5 cm long from Indian Head Point, St. Charles Bay, (5) wolfberries—>50 berries from ≥10 different plants from Sundown Bay, and (6) blue crabs—2–3 crabs (carapace width >10 cm) from Long Lake.

We multiplied average nutrient values for foods by the appropriate digestibility coefficients and ranked foods for available nutrient on a dry-weight basis. Digestion coefficients for *Rangia* clam have been used in calculations for stout razor clam, assuming that digestibilities for these clam species are similar. Ripe acorns collected from Dagger Point had fallen to the ground and were scorched during a prescribed burn several days before they

were collected and represented the type and quality of acorns Whooping Cranes ate (Hunt 1987). We used nutrient values of these acorns in food quality calculations.

Nutritional analyses were conducted using fresh excreta samples (lipid analysis) and dried ground excreta, feed, and food samples. Digestibility calculations for excreta and feed nutrient are expressed on a dry-matter basis corrected to standard drying time (3 h) and temperature (125°C) (Pomeranz and Meloan 1987). Calculations for food nutrient and total energy and nutrient availability of whole foods are expressed on a dry-weight basis.

Gross energy was determined using a Parr micro-bomb adiabatic calorimeter. Gross energy for *Rangia* clam was too low to be accurately determined by bomb calorimetry, and energy values were determined by multiplying percent crude protein by 4000 $cal \cdot g^{-1}$ and percent total lipid by 9000 $cal \cdot g^{-1}$ and adding the results. Total nitrogen was determined by the micro-Kjeldahl method (Helrich 1990). Crude protein was calculated by multiplying total Kjeldahl nitrogen by 6.25. Total lipids were determined by chloroform/methanol extraction for samples homogenized 4 min in a mechanical homoginizer (Folch et al. 1957). Total lipid in freshly homogenized foods was 6% less than for dried ground foods, and total lipid in fresh excreta samples was 4% less than for dried ground excreta samples. Drying foods and excreta at low temperatures and grinding did not lower lipid yield, but enhanced lipid yield compared to extraction of fresh samples. Uric acid was determined colorimetrically for dried excreta samples (Marquardt 1983). Chromium was determined by atomic absorption spectrophotometry after excreta samples were ashed in a muffle furnace and digested in nitric acid (Helrich 1990). Ash was determined by combusting dried samples for 4 h at 500°C in a muffle furnace (Helrich 1990). Total phenols were determined colorimetrically using a gallic acid standard for dried acorn and wolfberry samples extracted 30 min in 70% aqueous acetone (Singleton and Rossi 1965, Hagerman 1988). We determined chitin in blue crabs by sequential acid and alkali digestions (Black and Schwartz 1950).

Each bird was considered the unit of replication for statistical analysis of metabolizable energy and digestibility coefficients. Metabolizable energy and nutrient digestibility coefficients were analyzed for ranked data by three-way Kruskal-Wallis ANOVA (GLM procedure, SAS System) to test for the effects of study feed, Whooping Crane, and feeding trial on each variable. Kruskal-Wallis and Wilcoxon tests (SAS System) were conducted using ranked data to test for nutrient differences between feed ingredients and foods collected from Whooping Crane foraging areas. We compare nutrients of foods collected from Whooping Crane foraging areas by Kruskal-Wallis tests. Tukey's means comparison procedure was used for the separation of means when ANOVA results were significant. Means differences are reported at $P < 0.05$.

RESULTS

Food consumption rarely exceeded 200 $g \cdot day^{-1}$, indicating that sufficient feed was provided to study birds. Study birds maintained body weight during feeding trials from 0–2.3% of their body weight at six days after the initial move. Differences of nutrient levels between test ingredients used in feeds and nutrients in food samples (for the same foods) were less than 10% but were significant in several instances (Table 1). At difference levels of 10%, nutrients in test ingredients were representative of nutrients in foods eaten by wild Whooping Cranes.

Chromic oxide indicator in fecal samples collected at 18:00 EST on day 1 of each feeding trial was 937× higher than indicator in fecal samples collected prior to first exposure to indicator-marked study feeds at

TABLE 1

GROSS ENERGY (kJ·g $^{-1}$), AND PERCENT ASH, CRUDE PROTEIN, AND TOTAL LIPID FOR TEST INGREDIENTS AND FOODS COLLECTED FROM THE ARANSAS NATIONAL WILDLIFE REFUGE (DRY-MATTER BASIS)[a]

Food item/location	Gross energy	Ash	Crude protein	Total lipid
Live oak acorn:				
Test ingredient	20.101 ± 0.174(5)A	2.64 ± 0.02(9)A	4.82 ± 0.03(9)A	6.99 ± 0.10(9)A
East Shore Road	19.076 ± 0.158(5)B	2.62 ± 0.13(9)A	4.46 ± 0.08(9)B	5.45 ± 0.36(9)B
Dagger Point	18.799 ± 0.032(5)B	2.37 ± 0.12(9)A	4.55 ± 0.15(9)B	3.53 ± 0.21(9)C
Rangia cuneata:				
Test ingredient	0.380 ± 0.013(5)A	96.50 ± 0.03(9)B	1.71 ± 0.03(9)A	0.24 ± 0.02(9)A
Indian Head Point	0.326 ± 0.015(5)B	96.87 ± 0.04(9)A	1.44 ± 0.02(9)B	0.24 ± 0.03(9)A
Wolfberry fruit:				
Test ingredient	20.953 ± 0.022(5)B	9.47 ± 0.51(9)A	16.75 ± 0.03(9)B	10.16 ± 0.28(9)B
Sundown Bay	21.430 ± 0.057(5)A	7.01 ± 0.07(9)B	19.46 ± 0.31(9)A	13.38 ± 0.19(8)A
Blue crab:				
Test ingredient	10.514 ± 0.088(5)A	50.03 ± 0.13(9)A	38.27 ± 0.16(9)B	4.35 ± 0.04(9)A
Long Lake	11.947 ± 0.415(5)A	43.59 ± 0.97(9)B	41.89 ± 0.72(9)A	5.28 ± 0.64(9)A

[a] For each food and within columns, means with a different letter are significantly different ($P < 0.05$), values are means ± one SE. The numbers in parentheses indicate sample sizes.

07:00 on day 1. Indicator in excreta at 18:00 on day 1 was not significantly different from indicator in excreta at 14:00 on day 1 (1-tailed *t*-test, $t = -.6165$, $P > 0.25$). This rapid passage rate indicates that the 2-day adjustment period was adequate to eliminate non-study feed prior to sample collection on day 3 for excreta nutrient analysis.

The metabolizable energy coefficient for *Rangia* clam was significantly higher than that for acorns, wolfberry, and blue crab (Table 2). Protein digestibility for blue crab was higher than that for acorns and wolfberry. Lipid digestibility was lower for wolfberry than for *Rangia* clam and acorns. There was no significant effect of feeding trial on metabolizable energy and digestibility coefficients, and Whooping Cranes did not differ in digestion efficiency.

There were significant differences in nutrients among foods (Table 3). Gross energy ranged from 21.430 $kJ \cdot g^{-1}$ for wolfberry to 0.326 $kJ \cdot g^{-1}$ for *Rangia* clam; crude protein ranged from 41.89% for blue crab to 1.44% for *Rangia* clam. Total lipid ranged from 13.4% for wolfberry to 0.2% for *Rangia* clam, and ash ranged from 96.9% for *Rangia* clam to 2.4% for acorns from Dagger Point.

Wolfberry ranked highest of the five foods for metabolizable energy and total lipid nutrient availability per kg food ingested (Table 4). Blue crab ranked highest of the five foods for crude protein availability.

DISCUSSION

Protein digestibility coefficients obtained for Whooping Cranes for acorns (48.9) and wolfberry (53.4) are lower than those for *Rangia* clam (69.4) and blue crab (75.2); and are similar to the lower digestibilities for plant protein when compared to animal protein (Karasov 1990). Total dry-matter digestibility of *Rangia* clam was lower compared to the other foods, reflecting the high percentage of ash (96.87%) in *Rangia* clam. High metabolizable energy, protein, and lipid digestibility coefficients are expected for shellfish where muscle comprises most of the readily digested dry material (Karasov 1990); the MEC* for *Rangia cuneata* (75.0) was similar (72–73) to the MEC* for intertidal polychaeta (*Pseudonereis variegata*), black mussels (*Choromytilus meridionalis*), and limpet (*Patella granularis*) (Hockey 1984, Karasov 1990).

The MEC* for whole live oak acorn (43.2) was lower than that for white oak acorn meat (*Quercus alba*) (66.0) consumed by Ruffed Grouse (*Bonasa umbellus*) (Servello et al. 1987), and that for pin oak (*Q. palustris*) acorn meat (55.3) and red oak (*Q. rubra*) acorn meat (57.3) consumed by Northern Bobwhites (*Colinus virginianus*) (Robel et al. 1979). Non-digestible cellulose and hemicellulose together comprise approxi-

TABLE 2

APPARENT METABOLIZABLE AND DIGESTIBLE ENERGY, DRY MATTER, CRUDE PROTEIN, AND TOTAL LIPID DIGESTIBILITY COEFFICIENTS (%)[a]

Factor	Digestibility coefficients				
	Crane breeder feed	*Rangia cuneata*	Live oak acorn	Wolfberry fruit	Blue crab
Metabolizable energy	69.2 ± 1.0(5)A	75.0 ± 4.7(5)A	43.2 ± 3.8(5)B	44.8 ± 4.0(5)B	34.1 ± 6.3(5)B
Digestible energy	72.5 ± 1.0(5)A	76.7 ± 5.3(5)A	43.3 ± 3.5(5)B	43.8 ± 4.1(5)B	43.0 ± 5.4(5)B
Dry matter	90.1 ± 0.3(5)A	48.8 ± 3.3(5)C	80.2 ± 0.9(5)B	91.5 ± 1.1(5)A	71.2 ± 3.3(5)B
Crude protein	69.6 ± 2.4(5)AB	69.4 ± 4.4(5)AB	48.9 ± 5.4(5)C	53.4 ± 5.7(5)BC	75.2 ± 3.5(5)A
Total lipid	80.9 ± 1.1(5)AB	75.3 ± 5.7(5)AB	87.2 ± 3.9(5)A	60.0 ± 4.2(5)C	67.1 ± 5.4(5)BC

[a] Means within rows with different letters are significantly different ($P < 0.05$), values are means ± one SE. The numbers in parentheses indicate sample sizes.

TABLE 3

GROSS ENERGY (KJ·G^{-1}), AND PERCENT MOISTURE, ASH, CRUDE PROTEIN, TOTAL LIPID, TOTAL PHENOLS, AND CHITIN[a]

Component	Live oak acorn (East Shore Road)	Live oak acorn (Dagger Point)	Wolfberry fruit (Sundown Bay)	Blue crab (Long Lake)	Stout razor clam (Matagorda Island)	*Rangia cuneata* (Indian Head Point)
Gross energy	19.076 ± 0.158(5)B	18.799 ± 0.032(5)B	21.430 ± 0.057(5)A	11.947 ± 0.415(5)C	4.397 ± 0.049(5)D	0.326 ± 0.015(5)E
% Moisture	41.18 ± 1.87(9)D	17.41 ± 0.91(9)F	76.28 ± 0.25(9)A	72.96 ± 1.09(9)B	56.86 ± 0.46(9)C	26.79 ± 0.38(9)E
% Ash	2.62 ± 0.13(9)E	2.37 ± 0.12(9)E	7.01 ± 0.07(9)D	43.59 ± 0.97(9)C	78.55 ± 0.41(9)B	96.87 ± 0.04(9)A
% Crude protein	4.46 ± 0.08(9)D	4.55 ± 0.15(9)D	19.46 ± 0.31(9)B	41.89 ± 0.72(9)A	14.34 ± 0.37(9)C	1.44 ± 0.02(9)E
% Total lipid	5.45 ± 0.36(9)B	3.53 ± 0.21(9)C	13.38 ± 0.19(8)A	5.28 ± 0.64(9)B	1.74 ± 0.05(9)D	0.24 ± 0.03(9)E
% Total phenols	5.48 ± 0.37(9)B	7.25 ± 0.62(9)A	0.51 ± 0.04(9)C	—	—	—
% Chitin	—	—	—	6.92 ± 0.37(9)	—	—

[a] Means within rows with a different letter are significantly different ($P < 0.05$), values are means ± one SE. The numbers in parentheses indicate sample sizes.

TABLE 4
TOTAL ENERGY AND NUTRIENT AVAILABILITY (DRY-WEIGHT BASIS)

Food	Metabolizable energy ($kJ \cdot g^{-1}$)	Grams nutrient available per kg food ingested	
		Crude protein ($g \cdot kg^{-1}$)	Total lipid ($g \cdot kg^{-1}$)
Wolfberry fruit	9.601	104	80
Live oak acorn	8.121	22	31
Blue crab	4.074	315	35
Stout razor clam	3.298	100	13
Rangia cuneata	0.245	10	2

mately 27% of the total dry matter of whole live oak acorns (Short 1976), and the lower MEC* for whole live oak acorns was expected.

Tannins in foods inhibit protein digestibility (Marquardt and Ward 1979, Robbins et al. 1987, Johnson et al. 1993) and contribute to lower energy utilization in avian species (Servello and Kirkpatrick 1989, Johnson et al. 1993). Total phenolics are lower for acorns of the white oak group (includes live oak) than for acorns of the red oak group (Servello and Kirkpatrick 1989). However, total phenolics (>5%) in live oak acorns collected from the ANWR is high enough to affect protein digestibility and energy utilization by Whooping Cranes, as indicated by the low MEC* and protein digestibility for acorns compared to other foods.

Acorns, wolfberry, blue crab, stout razor clam, and *Rangia* clam were markedly different in nutrient composition (dry-weight). We divided Whooping Crane foods into two categories, (1) high energy-low protein and (2) low energy-high protein. Wolfberry and acorns are high in caloric content but lower in protein. Blue crab and stout razor clam are lower in calories, but have moderate to high protein levels. *Rangia* clam is low in energy and protein and is a suboptimal energy and nutrient resource for Whooping Cranes. Approximately 30× more *Rangia* clam, would have to be eaten than wolfberry and blue crabs to achieve comparable intake of metabolizable energy and protein.

Seasonal availability, relative size of food items, food density, and nutritional value must be considered when evaluating natural foods for Whooping Cranes. Acorns constitute a high-energy localized food resource. However, availability of acorns may be short compared to blue crab, wolfberry, and stout razor clam (Hunt 1987, Bishop et al. 1987, Stehn 1994b). Blue crab and stout razor clam provide 3–5× more digestible crude protein than wolfberry and acorns, are larger per unit capture, but are less localized and may require greater time for search and

processing. Wolfberry is small, and because plants are scattered, energy benefits for wolfberry may be offset by higher energy expenditure and lower rates of energy capture by foraging Whooping Cranes (pers. obs.).

Although we evaluated food quality on a dry-weight basis, moisture content among foods varied by as much as 438%. Variance in moisture of this magnitude may be significant if Whooping Cranes are limited in the amount of food they can consume and if feeding efficiency is affected by food availability. Acorns collected from Dagger Point averaged 17.4% moisture compared to 41.2% moisture for acorns collected along East Shore Road. On a wet-weight basis, metabolizable energy of acorns from Dagger Point was 6.699 $kJ \cdot g^{-1}$ compared to 4.699 $kJ \cdot g^{-1}$ for acorns from East Shore Road. Wolfberry ranked highest of all foods for metabolizable energy on a dry-weight basis. However, on a wet-weight basis, wolfberry provided only 2.275 $kJ \cdot g^{-1}$ compared to 6.699 $kJ \cdot g^{-1}$ for burned acorns.

Under some conditions of food availability, Whooping Cranes on the ANWR may have difficulty in meeting maintenance requirements and building energy reserves needed for spring migration (Iverson and Vohs 1982, Krapu et al. 1985). Foods may have been less available during fall and winter of 1993–1994, because acorns and blue crabs were not common, although wolfberry was abundant into January (Stehn 1994b). Whooping Cranes rarely fed on clams during winter 1993–1994 because refuge clam populations were lower in recent years (Stehn 1994b). Whooping Cranes were more dispersed in 1993–1994, and movements were less predictable, suggesting possible shortage of blue crab (Stehn 1994b). Cranes also migrated late during spring 1994, and an unprecedented 15 cranes remained on the refuge and Matagorda Island until early May (Stehn 1994b). Whooping Crane mortality was also higher than normal: three adults and five juveniles disappeared between 29 November 1993–16 February 1994 (Stehn 1994b). Counts in late 1994 included 131, down five from the spring departure count of 136 (Stehn 1994a). In spring 1993, a record 46 pairs nested; however, only 28 pairs initiated nesting in spring 1994 of a possible 45 known adult pairs (Stehn 1994a).

Multiple factors contribute to Whooping Crane mortality; predation, collisions with power lines, disease, and habitat conditions on the breeding ground (Brown et al. 1987, Garton et al. 1989, Kuyt et al. 1992, U.S. Fish and Wildl. Serv. 1994). It is possible, however, as indicated by the high over-winter mortality for 1993–1994, the late spring migration, lower number of returning Whooping Cranes, and low number of pairs that nested spring 1994, that food shortage on the ANWR was a contributing factor to low reproduction and high Whooping Crane mortality from late fall of 1993 to fall of 1994. Conditions of food shortage on the ANWR, similar to those observed during winter 1993–1994, are of concern if the

observed higher mortality and low reproductive success are related to lowered fitness caused by limited winter foods and the inability to assemble required energy reserves for migration and breeding.

ACKNOWLEDGMENTS

We especially appreciate the help of the caretaker staff at the Endangered Species Research Branch, PESC, that contributed to the success of working with captive Whooping Cranes. We also thank the staff at the ANWR for providing valuable logistic and advisory support. K. L. Risenhoover and D. M. Gatlin generously provided laboratory space and equipment at the Texas A&M Univ., Fish Nutrition Laboratory and Habitat Laboratory in the Dept. of Wildlife and Fisheries Sciences. The project was funded by the U.S. Fish and Wildlife Service.

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Wilson Bull., 108(4), 1996, pp. 740–747

TERRITORIES AND CACHING-RELATED BEHAVIOR OF RED-HEADED WOODPECKERS WINTERING IN A BEECH GROVE

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Abstract.—We describe caching and related behavior of Red-headed Woodpeckers (*Melanerpes erythrocephalus*) wintering in a beech grove during a mast year and relate territorial behavior and territory size to territory-specific mast abundance. We found no difference between territories of adults and juveniles in either territory size or abundance of mast. Rates of caching and social interaction decreased over the course of the winter. *Received Oct. 1995, accepted 8 Mar. 1996.*

Red-headed Woodpeckers (*Melanerpes erythrocephalus*) are larder hoarders during the fall and winter (Bent 1939, Kilham 1983). In autumn, these birds aggregate and establish singular winter territories at sites of high mast production (Smith and Scarlett 1987). Each territorial bird sequesters mast in one or a few larder trees which are then defended both inter- and intraspecifically. Red-headed Woodpeckers are known to store mainly acorns and beechnuts and an occasional insect (Hay 1887, Agersborg in Beal 1911, Kilham 1983). While acorn storing has been described for Red-headed Woodpeckers in Maryland, Louisiana, and Florida by Kilham (1983), MacRoberts (1975), and Moskovits (1978), respectively, no quantitative data exist on the storage of beech mast by this species. The present study describes caching and related behavioral patterns of Red-headed Woodpeckers wintering in a beech grove during a mast year and relates territorial behavior and territory size to territory specific mast abundance. We also searched for differences in behavior and territories between juvenile and adult woodpeckers.

METHODS

From 1 Nov. 1992 to 19 Mar. 1993 we observed 14 Red-headed Woodpeckers (6 juveniles and 8 adults) for a total of 160 h in a woodlot located in Morrow County, Ohio. The woodlot was dominated by mature American beeches (*Fagus grandifolia*), red maples (*Acer rubrum*), and sugar maples (*A. saccharum*). Other tree species at this site were white oak (*Quercus alba*), red oak (*Q. rubra*), ash (*Fraxinus* sp.), ironwood (*Carpinus* sp.), and hickory (*Carya* sp.). Beech was the only tree species experiencing a "mast year." We used focal bird techniques to gather behavior data. We watched each focal bird for 10-min periods. For the first 240 sec of this period, we noted which category of activity the bird was engaged in every 10 sec (N = 25). The five mutually exclusive categories were (1) lookout–the bird was perched and alert, (2) flight—the bird was in flight, (3) bipedal locomotion—the bird

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was moving over a tree, (4) peck—the bird was actively pecking, and (5) preen—the bird was preening. In addition to these five categories, we also recorded whether the bird was actively caching or engaged in any type of visual and/or auditory signaling or locomotory interaction. If the bird was caching, we noted whether the bird was on a trunk, limb, branch, or a twig, each of the last three substrate categories being an offshoot of the previous one. Visual displays consisted of an agonistic pose (Kilham 1983) or head bobbing. The display vocalization we witnessed has been described as "quirr" by Kilham (1958b). A chase was defined as one bird flying after another.

Over 10-min periods, we recorded the number of caches a focal bird made and every (previously-numbered) tree it visited. Temperature (°C), wind velocity (m/sec, Velometer Jr., Alnor Instrument Company, Niles, Illinois), solar radiation (mW/cm^2; Solar Meter, Dodge Products, Houston, Texas), and any precipitation were recorded for each observation period.

Juveniles could be distinguished from adults by plumage. Although the birds were not individually marked, we were able to identify individuals by idiosyncratic plumage patterns and behavior, as did Kilham (1958a).

We estimated the size of the beech crop by sampling fallen mast as follows: over a two-day period in early December, we gathered mast and leaf litter from below each beech tree in every bird's territory. For each tree, we gathered all leaf litter and mast within a 1660-cm^2 circular area located half way between the trunk and the outer edge of the canopy in each of the four cardinal directions. The samples were bagged and later sorted to determine number of beechnuts. Infertile nuts were excluded from the count.

Using a compass and a range finder, we constructed a map of all the marked trees in the study area. Each territory was delineated as the minimum-area polygon that included all the trees visited by the same bird. We drew each polygon to connect the positions of trunks, not canopy boundaries, a procedure that underestimated territory sizes. The polygons were then digitized and territory areas calculated.

The individual bird was the primary sampling unit, and all observations of the same individual were averaged before being analyzed. The data met the requirements for parametric tests.

To increase degrees of freedom when general linear models were employed, the individual bird was included as a factor. General linear models were performed in a stepwise fashion with the individual bird, time of day, day of winter (1 Nov. = day 1), average temperature, average wind speed, and average solar radiation included as independent variables. Only the independent variables retained in the model are reported. All statistical calculations were performed using Minitab (Anonymous 1991) or Systat (Wilkinson 1992) software.

RESULTS

Probable mortality between November and March was low (7%). The only bird disappearing during the study was a juvenile, and its territory was not usurped or occupied by any other Red-headed Woodpecker.

We could find no differences in the wind speed, temperature, or solar radiation associated with adult and juvenile territories (Table 1). There was no significant difference in size between territories of juveniles and adults (Table 1; Fig. 1). Neither the number of beechnuts per territory nor beechnut density was significantly different between the two woodpecker age classes (Table 1). We could find no difference between adult and juvenile birds in either the number of beech trees or the total number of trees defended (Table 1). Power analyses of these tests demonstrated

TABLE 1

MEAN ± SD FOR VARIABLES ASSOCIATED WITH ALL RED-HEADED WOODPECKER, JUVENILE RED-HEADED WOODPECKER AND ADULT RED-HEADED WOODPECKER TERRITORIES[a]

Variable	Total (N = 14)	Juvenile (N = 6)	Adult (N = 8)	*P*	Sample sizes from power analysis
Wind speed (m/sec)	0.9 ± 0.2	0.9 ± 0.1	0.9 ± 0.3	0.75	23
Temperature (°C)	1.4 ± 2.2	0.5 ± 2.5	2.0 ± 2.1	0.27	938
Solar radiation (mW/cm^2)	4.1 ± 3.6	3.7 ± 1.6	4.3 ± 1.2	0.48	316
Territory size (ha)	0.04 ± 0.03	0.03 ± 0.03	0.05 ± 0.03	0.28	236
Number of beech trees	4.8 ± 2.7	4.2 ± 2.4	5.3 ± 2.9	0.47	127
Total trees	8.9 ± 3.8	8.3 ± 2.3	9.4 ± 4.8	0.49	75
Beechnuts/territory[b]	24.5 ± 13.4	19.3 ± 15.0	28.3 ± 11.6	0.23	127
Beechnuts/m^2	62.3 ± 26.4	62.6 ± 31.4	62.0 ± 24.8	0.97	75
Interspecific interactions/min	0.23 ± 0.13	0.21 ± 0.09	0.2 ± 0.2	0.73	137

[a] *P*-values are significance levels of *t*-tests between juveniles and adults. The listed sample sizes from power analysis are those that would be required to detect a difference between juvenile and adult territories at $\alpha = 0.05$ and $\beta = 0.05$ given a 25% detectibility threshold and the current coefficient of variation.

[b] In thousands.

that detecting a significant difference with $\alpha = 0.05$ and $\beta = 0.05$ would require sample sizes of 23 to 316 (Table 1). Thus, our non-significant differences were probably not due to small sample sizes alone. There was some tendency for juvenile territories to be on the edge of the woodlot (Fisher's exact test, $P = 0.09$).

Although Red-headed Woodpeckers sometimes collect mast from the ground (TCG, pers. obs.), all of the birds we watched cached beechnuts gathered only from trees. Often, newly-collected beechnuts were broken on an "anvil", any portion not eaten immediately was stored. Although harvested corn fields were nearby, we never saw corn being gleaned and cached. The birds usually cached beechnuts on a trunk (30.9%), limb (43.9%), or branch (24.3%) and seldom on a twig (1.2%). There was no difference between caching rates of juveniles and adults, but over the months, the caching rate did decline for all birds (Fig. 2). A general linear model with the individual bird as a factor to account for the variation among individuals, and with day of winter as a covariate, showed that day of winter had a significant negative association with caching rate ($t = -3.48$, df = 135, $P = 0.001$).

There was no statistical difference between activity budgets of adults and juveniles. The birds spent most of their time looking about (69.9 ± 9.6%), with the rest of their time being divided among pecking (15.6 ± 8.7%), flying (8.6 ± 2.9%), bipedal locomotion (5.8 ± 2.4%), and preen-

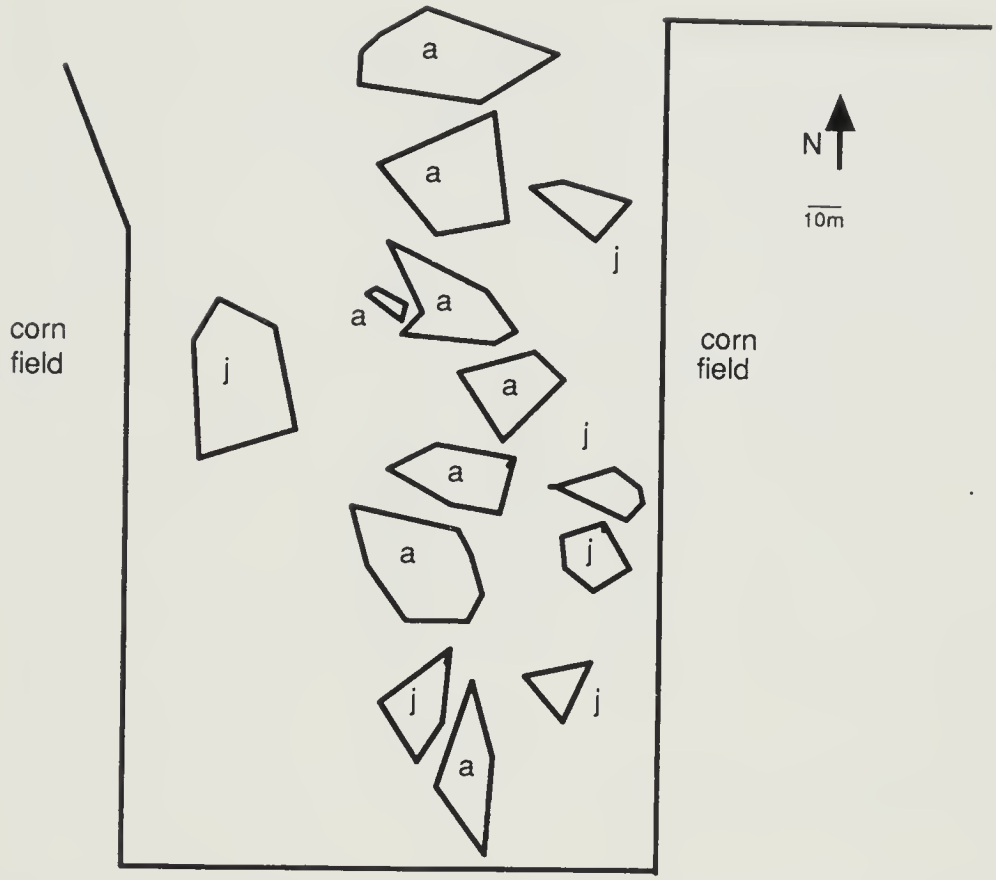

FIG. 1. Study area and Red-headed Woodpecker territories. A and J denote territories of adults and juveniles, respectively.

ing (0.2 ± 0.1%). A general linear model, with time spent looking about as the dependent variable, and day of winter and individual bird as factors showed that the percentage of time looking about increased as the winter progressed ($t = 4.13$, df = 135, $P < 0.000$).

The territories we observed were very small, about 0.05 ha (Table 1). Across the mosaic of territories, we witnessed 50 agonistic interactions involving Red-headed Woodpeckers. Nineteen of these were between Red-headed Woodpeckers, 13 were with Blue Jays (*Cyanocitta cristata*), 11 consisted of a Red-headed Woodpecker chasing mixed-species foraging flocks, six occurred with individual Carolina Chickadees (*Parus carolinensis*), Tufted Titmice (*P. bicolor*), white-breasted Nuthatches (*Sitta carolinensis*), or Downy Woodpeckers (*Picoides pubescens*), and once we witnessed a Red-headed Woodpecker chase off a fox squirrel (*Sciurus niger*). We could find no difference between juveniles and adults in the rate of interspecific interactions (Table 1). Although Red-bellied Woodpeckers (*Melanerpes carolinus*) resided in the woods just north of the study site, we rarely saw them and never witnessed them interacting with

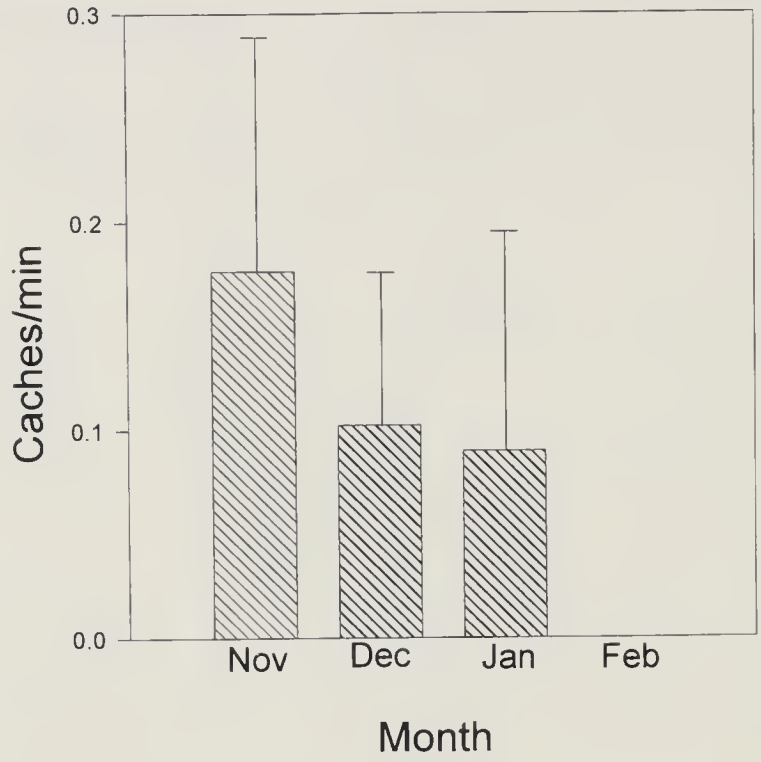

FIG. 2. Mean ± SD number of beechnuts cached per minute by Red-headed Woodpeckers wintering in a beech grove. N = 14.

M. erythrocephalus. Even though they are larger, Red-bellied Woodpeckers are socially subordinate to Red-headed Woodpeckers (e.g., Williams and Batzli 1979).

Behavior during agonistic interactions consisted of only a visual display (1.7%), vocalization with or without a visual display (72.1%), or chasing with or without a vocalization (26.2%). The frequency of interactions decreased over the course of the winter. A general linear model performed with percentage of 10-min recording periods lacking any social interaction as the dependent variable, individual bird as a factor, and day of winter as a covariate showed that the percentage of time devoid of social interaction increased with time ($t = 3.10$, df = 135, $P = 0.002$).

DISCUSSION

The average territory size of 0.04 ha was considerably smaller than that reported by Kilham (1958b, 0.1–0.2 ha), MacRoberts (1975, 0.8–1.2) or Moscovits (1978, 0.97 ha), although Moskovits did have a few territories as small as 0.04 ha. MacRoberts (1975) hypothesized that territory size is highly compressible and negatively correlated with mast production. This would seem to be so, but, unfortunately, other studies (including MacRoberts 1975) have no data on mast production (but see Smith and

Scarlett 1987). T.C.G. does have unpublished records pertaining to this point from two consecutive winters (1983–1985) when an index of beech mast was taken in the same woodlot with similar methods. During 1983, beech mast density was estimated at 231.1 nuts/m^2 and Red-headed Woodpecker density at 2.4 ± 0.2 birds/ha. The following year when beech mast was estimated at 57 ± 7.5 nuts/m^2, the woodpecker density was 3.6 ± 0.3 birds/ha. Such an increase in Red-headed Woodpecker density during a lower mast year contradicts both MacRoberts' (1975) assertion and Smith and Scarlett's (1987) data. Other potentially causal factors, such as differing mast levels in neighboring woods and/or differing woodpecker reproduction in previous summers could account for this disparity.

Although Kilham (1958a) thought that adults held smaller, more easily defended and "more desirable" areas, we could not support this assertion, nor could Moskovits (1978) find any difference between adult and juvenile territory sizes. There may have been some tendency for juvenile territories to be on the edge of the woodlot, a trend apparent in Kilham's (1958a) study area in Maryland where all juvenile territories bordered an old field (Kilham 1958a). Kilham (1958a) thought there were more dead trees for roosts and mast storage in the territories of adults. Such a disparity might account for the distribution of adult and juvenile territories in his study area, because the east side of his study area (where more of the adults were located) had many more dead locust trees. In our study area, there were few dead trees; the Red-headed Woodpeckers roosted in holes in dead limbs of living trees. We could find no difference in either the total number of trees or number of beech trees defended by juvenile and adult birds.

If, indeed, the territories of juveniles tend to be concentrated on the edge of woodlots, another possible explanation is that the winter microclimate on the edge of a wood is more severe than in the interior, with juveniles forced to take the lesser quality habitat. However, we could find no difference in the wind speed, temperature, or solar radiation associated with juvenile or adult territories that might support this idea.

Another way in which edge (juvenile) territories could be inferior relates to the number of intruders. Often, intruding birds were chased from territory to territory until they left the study area. Each successive woodpecker would be alerted by an intruder's interactions with other territory holders. The only Red-headed Woodpecker that would have no warning would be the initial bird, and so those occupying edge territories may have suffered more from the effects of intrusions. However, in compensation, owners of edge territories would benefit from fewer intraspecific interactions than owners of central territories. Since 19 of the 50 inter-

actions we observed (38%) were intraspecific, such an advantage could accrue to individuals on the edge of the territorial mosaic.

Kilham's (1958a) and MacRoberts' (1975) reports on Red-headed Woodpeckers in Maryland and Louisiana suggest that the birds closely monitor the acorn crop when selecting winter habitat. Willson's (1970) and Reller's (1972) observations in Illinois found them less dependent on mast crops and acting more as generalists by also feeding on insects. The local distribution and activity budgets of the birds we studied suggested that they were almost totally dependent on the stored beech mast crop for winter food.

MacRoberts (1975) reported that Red-headed Woodpeckers retrieved acorns from the ground. Only twice did we see a Red-headed Woodpecker on the ground and never in conjunction with mast collection. Even at the end of our study period, there were still beechnuts in the canopy, so there appeared to be no need for the woodpeckers to descend to the ground for food.

In our study area, all of the nuts an individual bird cached were apparently taken from within its territory. MacRoberts (1975) had similar findings, but in Kilham's (1958a) and Moscovits' (1978) studies, nuts were brought from a distance, sometimes from communal gathering areas as far as 100 m away from an individual's territory. Perhaps, in their study areas the distributions of cache sites and cachable food did not overlap to the extent evident at our study site.

The Red-headed Woodpeckers spent most of the late fall and early winter caching nuts. Time spent looking about and the percentage of time with no interactions increased as the winter progressed. Also, the rate of caching decreased over the winter as the birds became more sedentary and focused their behavior at a favorite site, only leaving to intercept intruders. Thus, the birds appeared to spend less time caching and more time guarding their caches once their territories had been established and stocked with provisions. Even within their extremely small territories, the birds spent most of their time in a "core" area centered on their storage area, as reported by MacRoberts (1975).

The Red-headed Woodpecker is a very aggressive bird in the winter when it is defending its territories. We found it to dominate every interaction, as did Moskovits (1978). In MacRoberts' study (1975), the Red-headed Woodpeckers rarely trespassed, and territory boundaries were hard to delineate. Such was not the case in this study. Territory lines were readily defined. As soon as a bird ventured into another bird's territory, an interaction ensued.

Kilham (1958b) found that Red-headed Woodpeckers defended their entire winter home ranges both intra- and interspecifically, while Mac-

Roberts (1975) determined that the species defended only those areas immediately around cache sites. As in Kilham's study (1958a), the territories we observed were very small and more easily defended than those of MacRoberts' (1975) birds.

Kilham (1958a), Reller (1972), MacRoberts (1975) and Moskovits (1978) all commented on the prevalence of interactions with the Red-bellied Woodpecker. We did not find Red-bellied Woodpeckers to be major competitors.

Most of the interactions consisted of vocalizations. This was probably the most efficient means of communicating, since chasing was probably more expensive energetically and a visual display would probably have had a lower probability of being received. We did find the number of interactions decreased as the winter passed, as did Moskovits (1978).

ACKNOWLEDGMENTS

We thank Randy Dettmers, Tim Kloth, Volodya Pravosudov, and Rodney Tienerand for help with the field work. Walter Riggs granted us permission to work on his property. This manuscript was improved by the comments of D. Ingold and D. F. Tombach.

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SEASONAL ABUNDANCE OF MIGRANT BIRDS AND FOOD RESOURCES IN PANAMANIAN MANGROVE FORESTS

GAËTAN LEFEBVRE AND BRIGITTE POULIN

ABSTRACT.—We studied temporal variation in abundance of Nearctic-Neotropical migrants, particularly the Northern Waterthrush (*Seiurus noveboracensis*), Prothonotary Warbler (*Protonotaria citrea*), and American Redstart (*Setophaga ruticilla*) in two black mangrove sites of central Panama from September 1993 through May 1995. The two sites, on the Caribbean and the Pacific coasts, differ importantly in annual rainfall, tide amplitude, and seasonal invertebrate abundance. Most migrant species varied temporally in abundance with the opposite pattern at each site, suggesting mid-winter movements correlated with abundance of food resources. Because of their wide geographic distribution and their particular response to hydrographic factors, mangroves are likely to have a temporally complementary role in sustaining migrant populations throughout the Neotropics. However, variations in migrant numbers reported in other Neotropical habitats could also reflect large-scale movements by migrants. Occurrence of mid-winter (facultative) migration has been documented mostly for the Palearctic-African migratory system, and needs to be investigated in the Nearctic-Neotropical realm for proper conservation of migratory species. *Received 17 Nov. 1995, accepted 16 April 1996.*

During the non-breeding period, Nearctic-Neotropical migrants generally use a succession of habitats. Movements between habitats are known to occur during the autumn and spring migrations, but most migrant populations are presumed to be spatially stable between these two periods (Rappole et al. 1993). Nonetheless, large variations in migrant abundance suggest that these movements occur throughout the non-breeding period in several Neotropical habitats (Galindo et al. 1963; Morton 1980; Emlen 1980; Hilty 1980; Johnson 1980; Orejuela et al. 1980; Greenberg 1984, 1992a; Blake and Loiselle 1992; Lefebvre et al. 1992; Sherry and Holmes 1996; Wunderle 1995). Although movements by migratory landbirds during the nonbreeding period have never been investigated in detail, a few lines of evidence suggest that they could be related to food abundance (e.g., Terrill and Ohmart 1984, Greenberg 1992a, Lefebvre et al. 1994b).

Mangrove forests are known to support high numbers of insectivorous migrants in several Neotropical regions (Russell 1980, Lynch 1989, Wunderle and Waide 1993, Lefebvre et al. 1994b). In particular, the Northern Waterthrush (scientific names in Table 1), the Prothonotary Warbler, and the American Redstart have been observed in mangroves of Mexico (Hutto 1980, Lynch 1989), Panama (Morton 1980), Colombia (Russell 1980),

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TABLE 1
NUMBER OF OBSERVATIONS OF EACH MIGRANT SPECIES AT TWO MANGROVE SITES

Species	Galeta (Atlantic)	Juan Diaz (Pacific)
Prothonotary Warbler (*Protonotaria citrea*)	200	222
Northern Waterthrush (*Seiurus noveboracensis*)	190	181
American Redstart (*Setophaga ruticilla*)	8	20
Black-and-white Warbler (*Mnioltila varia*)	13	7
Red-eyed Vireo (*Vireo olivaceus*)	17	1
Yellow Warbler (*Dendroica petechia*)	4	11
Chestnut-sided Warbler (*D. pensylvanica*)	9	0
Summer Tanager (*Piranga rubra*)	8	0
Tennessee Warbler (*Vermivora peregrina*)	5	2
Eastern Wood-pewee (*Contopus virens*)	4	2
Acadian Flycatcher (*Empidonax virescens*)	3	0
Canada Warbler (*Wilsonia canadensis*)	0	3
Blackpoll Warbler (*D. striata*)	1	1
Northern Oriole (*Icterus galbula*)	2	0
Golden-winged Warbler (*Vermivora chrysoptera*)	0	1
Blackburnian Warbler (*D. fusca*)	1	0
Bay-breasted Warbler (*D. castanea*)	0	1
Cerulean Warbler (*D. cerulea*)	0	1
Worm-eating Warbler (*Helmitheros vermivorus*)	1	0

Venezuela (Lefebvre et al. 1994b), and the West Indies (Arendt 1992, Wunderle and Waide 1993). Variation in species abundance and the birds' short length of stay (Lefebvre et al. 1992, 1994a) suggest that at least some individuals of these species undertake large movements during the nonbreeding period.

Mangroves are widely distributed in the Neotropics and often support more migrants than nearby terrestrial habitats (Hutto 1980, Lynch 1989, Wunderle and Waide 1993, Poulin et al. 1994). One possible explanation is that flooded habitats such as mangroves are buffered from the effect of rainfall seasonality and the resulting marked fluctuations in arthropod availability (Morton 1980, Lefebvre et al. 1994b, Sherry and Holmes 1996). Food available in mangroves is, however, likely to vary geographically and with latitude through the differing salinity and inundation patterns at each locality (Duke 1990, Lefebvre and Poulin, in press). Therefore, migrant species that use mangroves extensively as a wintering habitat could move between mangrove forests to take advantage of these temporal variations in food resource.

In this paper we compare the seasonal abundance of Nearctic-Neotropical migrants from two Panamanian black mangrove forests experiencing

different hydrographic conditions. In particular, we attempt to answer the following questions: Do migrant populations show large variation in abundance during the nonbreeding season? Are the two mangrove sites used differentially through time by migrants? Is variation in migrant abundance related to the abundance of food resources at each site?

STUDY AREAS AND METHODS

Study areas.—We carried out this study in two coastal mangrove forests 65 km apart in central Panama from September 1993 to May 1995. These were Juan Diaz (9°00′N, 79°04′W) on the Pacific coast and Galeta (9°20′N, 79°09′W) on the Caribbean coast. Each study site was 4.5 ha of black mangrove (*Avicennia germinans* L.) with red (*Rhizophora mangle* L.) and white (*Laguncularia racemosa* L.) mangroves comprising around 30%. Annual rainfall in Galeta (3244 mm) averages nearly twice that in Juan Diaz (1786 mm). The two sites also differ importantly regarding mean tidal range, with a value of 24 cm for Galeta and 395 cm for Juan Diaz. Both sites, however, experience a dry season of similar intensity from January to April which coincides with the period of lowest high tides (Lefebvre and Poulin, in press).

Bird abundance.—Migrant abundance was evaluated during observation sessions twice monthly from September 1993 through May 1994. To eliminate any short-term temporal bias, the two sites were sampled on two consecutive days. At each site, observations were carried out at 18 spot counts located 50 m apart along two transects. Starting at sunrise, we surveyed each spot for 10 min, and noted every new bird seen within 25 m.

Invertebrate abundance.—Abundance of invertebrates, the main food resource available to passerines in mangroves (Lefebvre et al. 1994b), was estimated during each observation session. The first 2 m of vegetation were swept with a standard insect net in late morning during 15 min. Sweep-netted invertebrates were preserved in 70% ethanol and sorted using a dissecting scope. Each invertebrate was identified to order or family and categorized as small (≤0.5 mm) or large (>0.5 mm). Sub-adult forms of insects were assigned either to eggs or larvae without taxonomic distinction.

Bird diet.—We determined diets of migrants through regurgitation sessions during two non-breeding seasons. We sampled sites alternately twice monthly so that regurgitations were collected during each calendar month at each site. Twelve mist-nests (10 m × 3 m, 32-mm mesh) were operated from dawn until early afternoon. Some 452 migrants from 14 species were captured and administered tartar emetic following the method of Poulin and Lefebvre (1995). Diet samples were preserved and sorted using the same methodology as for sweep-net samples.

Food abundance.—Using data from sweep-net and emetic samples, a monthly index of food abundance was calculated as follows:

$$\text{Index of food abundance} = \sum p_i \frac{x_i}{n_i}$$

where p_i is the proportion of a specific arthropod group (taxa/size) in migrants' diet, x_i is the number of arthropods from that group sampled with sweep net during a specific date, and n_i is the total number of arthropods from that group sampled with sweep net. Accordingly, this index reaches a maximal value when several arthropod groups extensively taken by the birds simultaneously show a high abundance.

Statistical analyses.—We used Spearman's correlation rank coefficient to compare temporal abundance in migrants between the two sites. We compared abundance of each ar-

thropod group (taxa/size) between the two sites with contingency tables using *G*-tests. All 18 sweep-net samples collected at each site were combined since they were independent samples without replicate. To determine whether changes in bird abundance between sites were correlated with changes in food abundance between sites, we subtracted bird and food abundances at one site (Juan Diaz) from the other (Galeta) for each sampling date throughout the nonbreeding period and calculated Spearman correlations between the two data sets. Most data were pooled by month in presentation of figures, but all analyses were run on data collected twice each month.

RESULTS

Bird abundance.—Overall, 466 and 453 migrants from 15 and 13 species were observed at Galeta and Juan Diaz, respectively (Table 1). Nine species representing over 95% of all observations were sampled at the two sites. Both migrant communities were dominated by the Prothonotary Warbler and the Northern Waterthrush (Table 1). Most species showed large variations in abundance with a different temporal trend at each site (Fig. 1). Abundances of the Northern Waterthrush at Galeta and Juan Diaz were inversely correlated from October through March ($r_s = -0.713$, df = 10, $P < 0.01$), with higher numbers on the Pacific coast in early winter and on the Caribbean coast in late winter. The Prothonotary Warbler was abundant at both sites from September through January only. In Galeta, its abundance was high in September and gradually decreased during winter, whereas in Juan Diaz it was high and stable from October through January. Abundances of the American Redstart at Galeta and Juan Diaz were negatively correlated from November through March ($r_s = -0.792$, df = 9, $P < 0.05$), showing an inverse pattern to the one of the Northern Waterthrush. The remaining 16 migrant species were sampled only occasionally and were clumped in "other" migrant species (Table 1). Their abundances at Juan Diaz and Galeta were inversely correlated from September through May ($r_s = -0.566$, df = 13, $P < 0.05$). These migrants were sampled mostly during autumn migration at Juan Diaz and at the end of the wintering period at Galeta (Fig. 1).

Estimation of food resources.—Over 400 diet samples were collected (218 from Juan Diaz and 196 from Galeta), from which 3689 items were identified and assigned to one of 34 invertebrate groups (taxa/size) (Table 2). Over 98% of the invertebrates taken by migrants were from taxa also sampled by sweep net. Some 78% of these invertebrates were present in at least half of the 36 sweep-net samples. In Galeta, migrants fed mostly on small beetles, small ants, large insect larvae, and small spiders, whereas in Juan Diaz small snails, beetles, and ants were the most common invertebrates in migrants' diet (Table 2).

Abundance of food resources.—Between-site comparisons in the index of food abundance show that food resources were more abundant in Juan

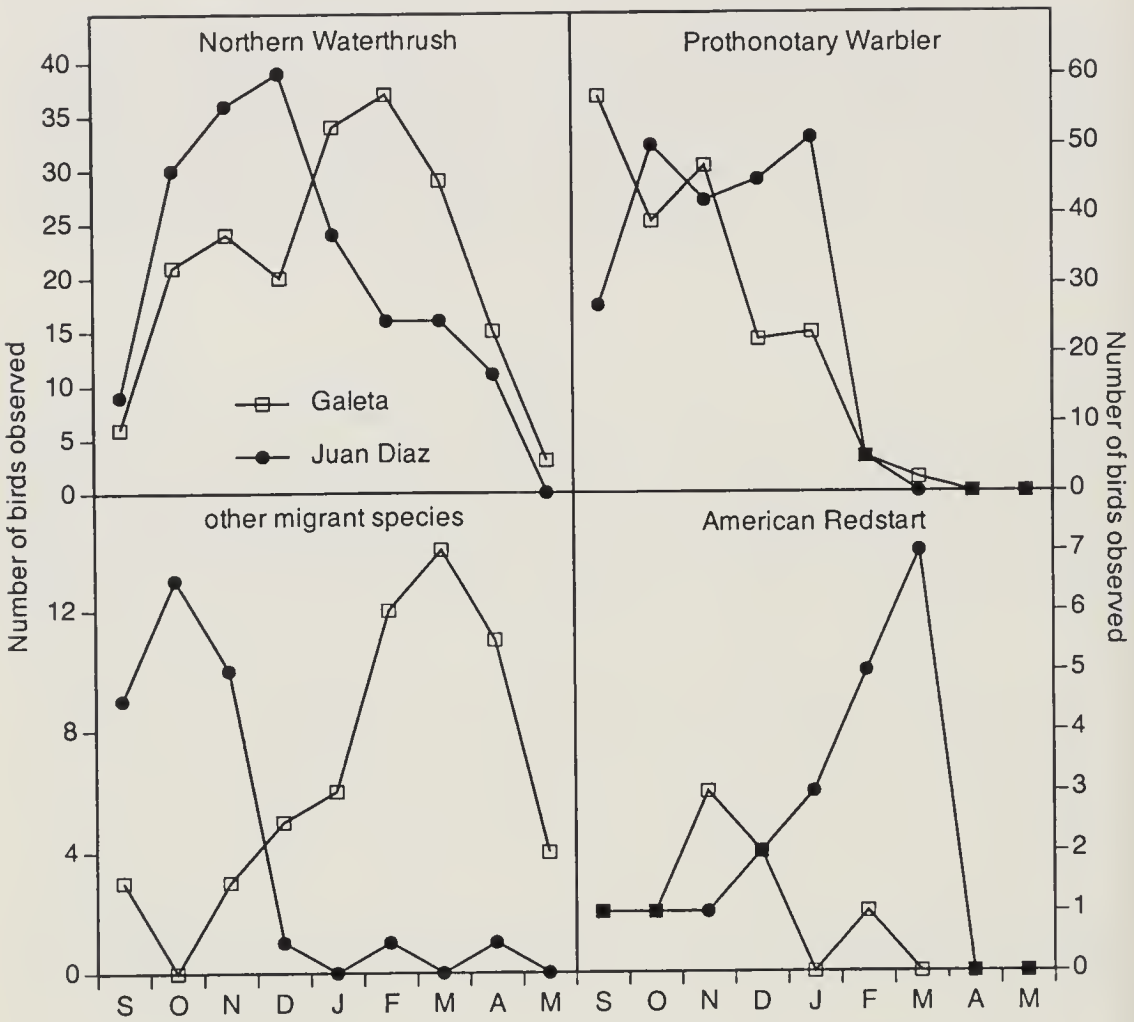

FIG. 1. Monthly abundance of migrant species at the two study sites.

Diaz from September to December (wet season) and more abundant in Galeta from January to April (dry season) (Fig. 2). Actually, several invertebrate groups (taxa/size) showed a significantly different abundance between the wet and the dry seasons, with an opposite trend at each site (Table 2). In Juan Diaz, nine invertebrate groups representing 53% of all invertebrates sampled were significantly more abundant during the wet season. In Galeta, 13 invertebrate groups representing 63% of all invertebrates sampled were significantly more abundant during the dry season.

Relationships between migrant and food abundance.—Concurrent changes in numbers of Northern Waterthrushes and in the index of food abundance were positively correlated between the two sites ($r_s = 0.5772$, df = 15, $P < 0.05$). No such relation was found for the Prothonotary Warbler ($r_s = -0.1545$, df = 11, $P = 0.94$) or the American Redstart ($r_s = -0.0168$, df = 11, $P = 0.96$). Between-site variations in abundance of

TABLE 2

SEASONAL VARIATION IN SWEEP-NET SAMPLES AND PROPORTION OF EACH INVERTEBRATE-PREY GROUP IN THE MIGRANT'S DIET

Taxa	Size	Sweep net WS vs DS[a]		Number of items in migrants' regurgitations (%)	
		Galeta	Juan Diaz	Galeta	Juan Diaz
Gastropoda (snails)	Small	***	=	65 (4.3)	1089 (49.8)
Gastropoda (snails)	Large	+	++	1 (0.1)	
Pseudoscorpionida	Small	=	=	10 (0.7)	5 (0.2)
Araneida (spiders)	Small	+++	**	127 (8.4)	41 (1.9)
Araneida (spiders)	Large	**	=	53 (3.5)	9 (0.4)
Isopoda	Small	=	*	1 (0.1)	13 (0.6)
Decapoda (crabs, shrimps)	Small	?	?	5 (0.3)	2 (0.1)
Decapoda (crabs, shrimps)	Large	?	?	3 (0.2)	4 (0.2)
Chilopoda (centipedes)	Large	=	?		1 (0.0)
Thysanura (bristletails)	Large	?	?		1 (0.0)
Odonata	Large	=	=	7 (0.5)	
Orthoptera	Small	=	***	5 (0.3)	4 (0.2)
Orthoptera	Large	+++	***	14 (0.9)	7 (0.3)
Dermaptera (earwigs)	Large	?	?		1 (0.0)
Heteroptera (true bugs)	Small	+++	=	15 (1.0)	9 (0.4)
Heteroptera (true bugs)	Large	=	***	8 (0.5)	1 (0.0)
Homoptera (plant bugs)	Small	+++	=	4 (0.3)	88 (4.0)
Homoptera (plant bugs)	Large	+	=	2 (0.1)	4 (0.2)
Coleoptera (beetles)	Small	+++	**	351 (23.4)	385 (17.6)
Coleoptera (beetles)	Large	=	***	13 (0.9)	9 (0.4)
Lepidoptera	Small	+++	=		1 (0.0)
Diptera (flies)	Small	**	**	12 (0.8)	15 (0.7)
Diptera (flies)	Large	=	=	1 (0.1)	2 (0.1)
Hymenoptera (ants)	Small	+++	=	294 (19.6)	321 (14.7)
Hymenoptera (ants)	Large	+++	+++	19 (1.3)	17 (0.8)
Hymenoptera (wasps)	Small	+++	=	87 (5.8)	76 (3.5)
Hymenoptera (wasps)	Large	+++	**	18 (1.2)	2 (0.1)
Insect eggs	Small	+++	+++	72 (4.8)	59 (2.7)
Insect eggs	Large	=	=	2 (0.1)	
Insect larvae	Small	+++	+++	42 (2.8)	13 (0.6)
Insect larvae	Large	=	=	266 (17.7)	7 (0.3)
Fishes	Large	?	?	5 (0.3)	
Frogs	Large	?	?		1 (0.0)
Lizards	Large	?	?	1 (0.1)	

[a] Comparison (*G*-tests) in numbers of sweep-netted invertebrates from the wet (WS; September through December) to the dry (DS; January through April) season. Increase: + ($P < 0.05$), ++ ($P < 0.01$), +++ ($P < 0.001$); no significant change: =; decrease: * ($P < 0.05$), ** ($P < 0.01$) *** ($P < 0.001$); ?: not sampled.

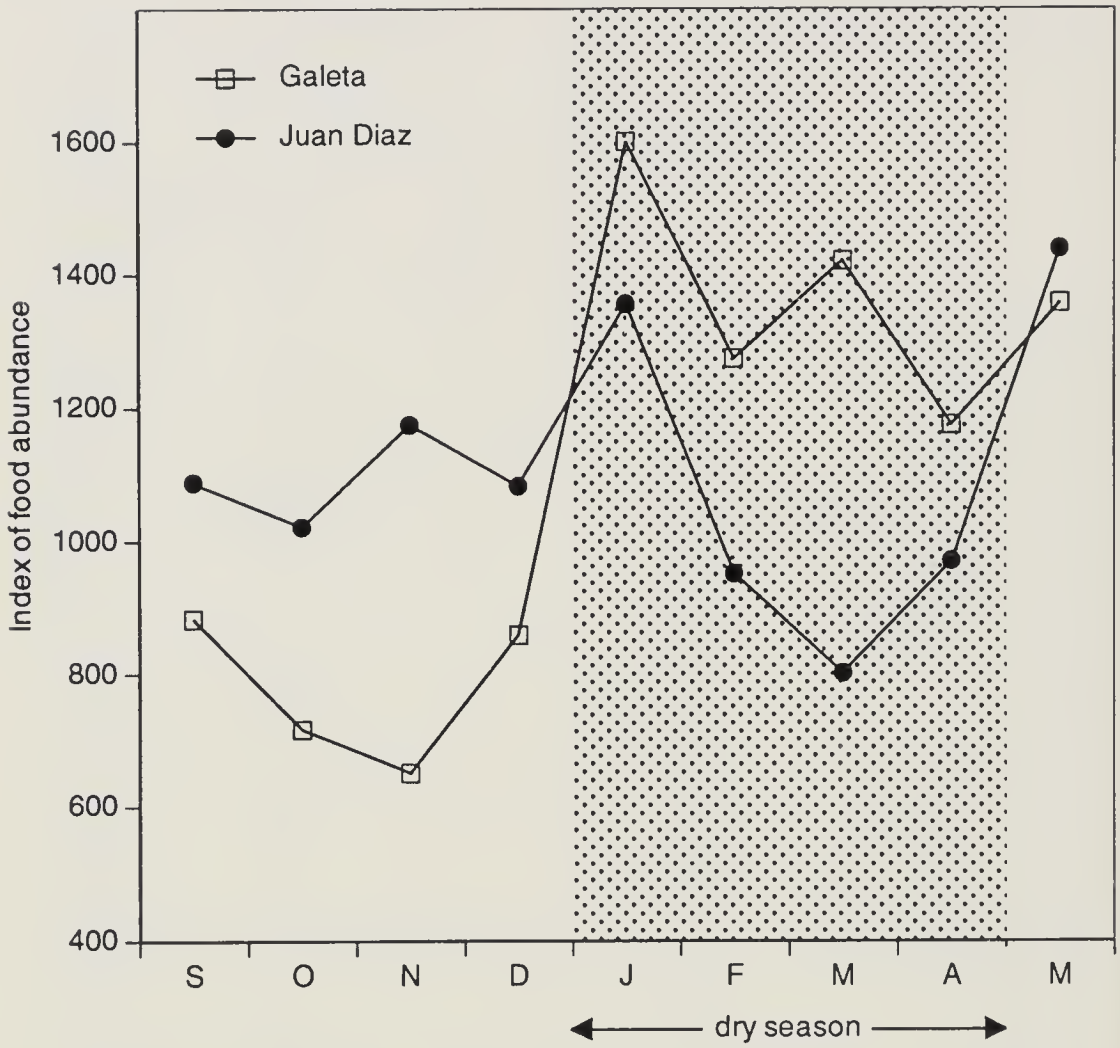

FIG. 2. Monthly variation in the index of food abundance at the two study sites.

other migrant species was positively correlated with between-site variations in the index of food abundance ($r_s = 0.7815$, df = 15, $P < 0.001$).

DISCUSSION

The two mangrove sites were used by a similar number of migrant birds. However, all species, with the exception of the Prothonotary Warbler, showed an opposite abundance pattern at the two sites. We do not pretend that these variations were related to bird movements from one mangrove site to another (no bird was captured at both sites), but our data suggest that the two mangrove sites have a temporally complementary role in sustaining migrant populations during their stay in central Panama.

Because of the differing tide and inundation patterns, rainfall seasonality affects differently the invertebrate fauna at the two mangrove sites

(Lefebvre and Poulin, in press). As a result, invertebrate abundance was higher in Pacific mangroves during the first part of the wintering period (wet season) and higher in Caribbean mangroves during the second part of the wintering period (dry season). This pattern was found in several groups of arthropods, including the ones frequently taken by the migrant species.

Between-site variations in abundance of Northern Waterthrushes were synchronised with between-site variations in food abundance. This species used extensively one mangrove only when food resources were proportionally more abundant than at the other, and its abundance at any site was low when food resources were proportionally less abundant.

Within and between site variations in abundance of Prothonotary Warblers were not correlated to abundance of food resources. This species was present only during the first part of the nonbreeding season when resources were relatively stable at both sites. However, the Prothonotary Warbler showed a different abundance pattern at the two sites, potentially reflecting differences in food abundance. In Juan Diaz, where resources were more abundant, the Prothonotary Warbler showed a high and uniform abundance. The departure of most individuals in February occurred when food abundance decreased sharply. In Galeta, where food resources were less abundant, abundance of Prothonotary Warblers decreased throughout the nonbreeding period.

The abundance pattern of the American Redstart suggests movements among mangrove patches, but these were not correlated with food abundance. This was especially notable at Juan Diaz, where bird abundance increased drastically during the dry season when resource abundance was low. The few regurgitation samples collected for this species show that the American Redstart, in contrast to other wood warblers, feeds extensively on small homopterans and insect eggs (76% of all food items taken). Small homopterans were more abundant in Juan Diaz than in Galeta (total in sweep-net samples: 422 vs 713, $G = 75.4$, df = 1, $P < 0.001$), even considering only the dry season when homopteran abundance increased in Galeta but remained stable in Juan Diaz (274 vs 377, $G = 16.4$, df = 1, $P < 0.001$). Small insect eggs were one of the few arthropod groups more abundant in the dry than the wet season at Juan Diaz.

The other migrant species showed large variations in abundance with an opposite pattern at each site. These species were predominantly found on the Pacific side during southward migration and on the Caribbean side during northward migration, which was positively correlated with variation in food resources at the two sites.

Large variations in migrant abundance occur in Panamanian man-

groves. Our data suggest that they are related to mid-winter movements associated with variation in food availability. The proximity of the Atlantic and Pacific coasts in Panama allowed the sampling of two mangrove sites experiencing different hydrographic conditions within a short range, but the variations observed in migrant abundance could conceal bird movements on a larger geographical scale. In coastal mangroves of Venezuela, the same warblers species exhibit large variations in abundance during the non-breeding period (Lefebvre et al. 1992). Because of their wide geographic distribution in the Neotropics and their particular response to hydrographic factors, mangroves are probably more likely to support large scale movements of migratory birds than other Neotropical habitats. However, and regardless of the fact that few studies have investigated seasonal variation in migrant abundance throughout the nonbreeding season, important changes in migrant numbers have been reported in grassland (Greenberg 1992a), pine forest (Emlen 1980), lowland second-growth forest (Blake and Loiselle 1992), lowland dry forest (Orejuela et al. 1980, Greenberg 1984, Sherry and Holmes 1996), lowland wet forest (Greenberg 1984), second-growth low mountain wet forest (Wunderle 1995), and low mountain wet forest (Johnson 1980) habitats. While these variations are often assumed to be associated with mortality or local habitat shifts, they could potentially reflect bird movements on a wide geographic distance. Nearctic-Neotropical migrants are more numerous and exploit a greater variety of winter habitats in the northern Neotropics (Terborgh and Faaborg 1980, Pashley and Martin 1988, Rappole et al. 1993) and are less numerous and more selective in their habitat choice farther south (Pearson 1980, Bosque and Lentino 1987, Wunderle and Waide 1993). Several studies carried out in the West Indies (Emlen 1980, Sherry and Holmes 1996, Wunderle 1995) and Central America (Galindo et al. 1963, Blake and Loiselle 1992, Greenberg 1992a) have reported a decrease in migrant abundance over the non-breeding season, whereas some habitats in South America support an increasing number of migrants throughout winter (Johnson 1980, Hilty 1980, this study). Considering the important changes occurring in food resources between the wet and the dry seasons in most Neotropical habitats (Poulin et al. 1992, Sherry and Holmes 1996), quality of the foraging microhabitat is likely to vary during the nonbreeding season. A migration in mid-winter could then represent an advantageous strategy for several migrant birds.

These migrations during the non-breeding period could correspond to facultative migrations which are directly in response to changes in environmental conditions and may or may not occur in any given year (Berthold 1975, Terrill 1990). Such migrations have been observed in long distance Palearctic insectivorous migrants (Gwinner et al. 1988, Wood

1979) and short distance Nearctic insectivorous migrants (Terrill and Ohmart 1984) experiencing an important decrease in food resources. Cage experiments have demonstrated that between fall and spring migrations, some insectivorous long distance migrants react to food shortage by night activity (*Zugunruhe*), similar to that observed during the obligatory migration phase (Terrill and Ohmart 1984, Gwinner et al. 1988). Actually, several lines of evidence suggest a much higher potential for extensive winter movement by migrants than has generally been considered to be the case (Curry-Lindahl 1981, Gwinner 1990, Terrill 1990).

Examples of winter site tenacity by migrants are numerous in the Neotropics (see Rappole and Warner 1980). However, the proportion of individuals exhibiting site tenacity within a species often varies among habitats (Greenberg 1984, Sherry and Holmes 1996, Wunderle 1995) and years (Emlen 1980, Greenberg 1992a, Wunderle 1995), potentially reflecting mid-winter migration by some individuals in response to a decrease in foraging microhabitat quality. Understanding seasonal changes in population and resource use is critical in providing efficient management policies for migratory birds (Greenberg 1992b, Sherry and Holmes 1995). Occurrence of multiple stage migrations has been documented, mostly for the Palearctic-African migratory system, and need to be investigated in the Nearctic-Neotropical realm for proper conservation of migrant species.

ACKNOWLEDGMENTS

The Natural Sciences and Engineering Research Council of Canada (NSERC) supported this study. We are grateful to the Smithsonian Tropical Research Institute for providing logistical support and to INRENARE (Instituto de recursos naturales renovables) for issuing the research permit to work in mangroves. We thank Stanley Rand, Neal Smith, and Russell Greenberg for providing helpful comments on this manuscript.

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Wilson Bull., 108(4), 1996, pp. 760–770

EFFECTS OF CONSERVATION RESERVE PROGRAM FIELD AGE ON AVIAN RELATIVE ABUNDANCE, DIVERSITY, AND PRODUCTIVITY

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Abstract.—Introduced grass dominated Conservation Reserve Program (CRP) fields were monitored in summer 1992 in Gratiot County, Michigan, to determine the relationship between field age and avian relative abundance, diversity, and productivity. Younger CRP fields (1–2 years old), best described as a combination of forbs and bare ground, had the greatest diversity and relative abundance of avian species. Older CRP fields (3–5/6 years old) were a combination of grasses and deep litter cover and had the greatest avian productivity. We recommend that after 3–5 growing seasons CRP fields be manipulated to provide a variety of successional stages to maintain simultaneously high avian relative abundance, diversity, and productivity. *Received 6 Nov. 1995, accepted 1 May 1996.*

Specialization and intensification of agricultural practices have contributed to dramatic declines in wildlife populations over the last 60 years (USDA 1972). These land-use practices have decreased the availability of cover types (i.e., number of grasslands and wetlands) available for many farmland wildlife species (Berner 1988). In the Midwest, agricultural practices that adversely impact wildlife are commonly used because the production of quality wildlife habitat provides reduced economic returns to farmers compared to commodity production (Langer 1979). To alleviate excess commodity production and to combat the effects of past agricultural practices, the federal government initiated land retirement programs beginning in the 1930s. These programs provided varying amounts and qualities of wildlife habitat (Berner 1988). The most recent land retirement program is the Conservation Reserve Program (CRP). The CRP provisions of the 1985 Food Security Act (Farm Bill) provide economic incentives to farmers to remove highly erodible and environmentally sensitive cropland from production for 10 years. Perceived benefits of this program include curtailing soil erosion and excess commodity production and creating wildlife habitat.

The CRP offers a unique opportunity to view the successional dynamics of grasslands and associated changes in wildlife populations for 10 years. Avian communities should provide insight into the quality of habitat provided by the CRP because avian species are excellent indicators of habitat quality and respond quickly to environmental changes (Graber

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and Graber 1976). Determining which age or ages of CRP fields support the greatest relative abundance, diversity, and productivity of avian species provides a framework on which management recommendations can be based. Once created and maintained, these grassland habitats should increase the above-mentioned avian variables in a landscape dominated primarily by less diverse agricultural monocultures. The objective of this study was to determine the relationship of various age classes of CRP fields to avian relative abundance, diversity, and productivity by quantifying vegetation structure and composition of CRP fields and the associated changes in avian variables.

STUDY AREA AND METHODS

Nineteen 6.5–20 ha study sites were selected in Gratiot County, Michigan, in 1992. Each CRP field varied in age from 1–6 years (1–4 [N = 3 in each], 5 [N = 6], and 6 years [N = 1]) and was planted to introduced grasses and legumes (alfalfa [*Medicago sativa*], orchard grass [*Dactlyis glomerata*], timothy grass [*Phleum pratense*], and clover [*Trifolium* spp.]) (Millenbah 1993). None of the fields in this study was mowed, grazed, burned, or disced since contract initiation.

Data collected in 1992 represent a time-specific analysis of different age CRP fields. Rather than use a cohort approach, where a sample of fields would be examined annually for a number of years, representatives from different age classes were observed within a year. Using this approach, two assumptions were made. First, it was assumed that all fields selected for observation received similar treatment. That is, all fields were planted in a similar manner to a similar mix of grasses and legumes, and no field had been disturbed since contract initiation. Second, it was assumed that weather had affected fields similarly. However, if there were differences among fields, for either assumption, it is likely that they were distributed randomly across age classes. Therefore, because both assumption were likely met, the time-specific approach provides an adequate representation of the changes in the measured variables as CRP fields age.

Vegetation structure and composition data were collected along six permanent 100 m long, systematically established transects in each field, with six sampling points per line. Sampling occurred every 20 m along each transect in May (peak avian breeding season). Horizontal cover was assessed 4 m from a Robel pole (Robel et al. 1970). Maximum height of living and standing dead vegetation was recorded at each sampling point. Percentage canopy cover of live and dead vegetation; percentage canopy cover of grasses, forbs, and woody vegetation; percentage litter cover; and percentage bare ground were assessed using a 50 by 50 cm sampling frame (modified from Daubenmire 1959). Frequency of all herbaceous species occurring within the sampling frame and litter depth were recorded at each sampling point.

Bird censuses were conducted in each field to determine relative species abundance and diversity. Counts were made from 1 May–15 August every two weeks. Censuses were made from transects spaced 50 m apart along the long axis of the field. Censuses were conducted from sunrise to three hours after sunrise. Counts were not made if it was raining or if wind speed exceeded 16 kph. Observers walked slowly along transect lines making frequent stops to scan for birds. All birds seen or heard were recorded. Only those birds observed within 25 m of either side of the transect were included in the census to minimize double counting. Relative bird abundance was reported as birds/ha.

Entire fields were searched for nests to quantify nesting success on different age classes

of CRP fields. Nine fields representing three age classes (1 [N = 3], 4 [N = 2], and 5 years old [N = 4]) were searched in mid-May and mid-June. Searches were conducted with 3–6 observers walking 1–2 m apart until fields had been completely traversed. Nests were revisited every 2–3 days until young had fledged or the nest was determined to be abandoned or destroyed. Incidentally discovered nest were also monitored.

Comparisons of vegetation variables and avian relative abundance and diversities among age classes within sampling periods and nesting success among age classes were made using Kruskal-Wallis (KW) one-way analysis-of-variance (Siegel 1956). A KW multiple comparison test (Miller 1980) was used to determine which field age classes were significantly different if there was a significant ($\alpha = 0.10$) KW result. Because there was only one 6-year-old field, this field was combined with 5-year-old fields for all statistical tests (hereafter referred to as 5/6) on avian relative abundance and diversity and vegetation variables.

Avian diversities were calculated using the Shannon-Weaver diversity index. Nest success (nests surviving from initiation of egg laying to fledging) was calculated using the Mayfield (1961) method.

Friedman's two-way analysis-of-variance (Siegel 1956) was used to test for differences among age classes for avian relative abundance and diversities over the census period (May–August). Blocking was done on the census period. A Friedman's multiple comparison test (Miller 1980) was used to determine which age classes were significantly different over the census period if there was a significant ($\alpha = 0.10$) Friedman's result.

Friedman's two-way analysis of variance also was used to test for differences in relative frequencies of dominant plant species among fields within an age class. The five plant species with the greatest relative frequencies on each field were included in the analysis. Failure to reject the null hypothesis would suggest that an age class of CRP field could be described by the dominant plant species present.

Principal components analysis (PCA) was used to examine the relationship between field age, vegetation characteristics, and avian relative abundance and diversities. Because measured vegetation variables may be related, PCA was used to reduce the number of variables to a few independent variables. The new variables, or principal components, were linear combinations of the original vegetation variables. The linear combinations maximized the variance in the data and could be used to identify the original variables most significant in describing a particular age of CRP field. Analysis was done using a correlation matrix.

RESULTS

Eighty-two plant species were identified on 19 CRP fields. Individual fields within each age class differed (Friedman, $P < 0.10$) in the relative frequencies of plant species identified. Therefore, a particular age of CRP field could not be described by the dominant plant species present. These findings preclude any meaningful test of changes in dominant plant species composition as fields age. Similarly, we observed no consistent successional replacement of dominant plant species as fields aged (Millenbah, unpubl. data).

Vegetation characteristics that differed significantly (KW, $P < 0.10$) among age classes included horizontal cover, percent total canopy, percent live canopy, percent dead canopy, percent grass canopy, percent forb canopy, percent litter cover, percent bare ground, and litter depth (Table 1). However, none of the significant differences was consistently related to

TABLE 1

MEAN (SE) VEGETATION CHARACTERISTICS ON DIFFERENT AGE CLASSES OF CONSERVATION RESERVE PROGRAM (CRP) FIELDS

Characteristic	Age class[N][a]				
	1[3]	2[3]	3[3]	4[3]	5/6[7]
Horizontal cover (dm)[b]	2.5^{A} (0.4)	3.6^{AB} (0.6)	3.3^{AB} (0.3)	4.1^{B} (<0.0)	3.1^{AB} (0.3)
Height of live vegetation (dm)	2.9 (0.5)	4.5 (0.9)	4.4 (0.5)	5.2 (0.2)	3.7 (0.4)
Height of dead vegetation (dm)	7.4 (0.7)	9.2 (0.4)	9.2 (1.1)	9.4 (1.4)	9.3 (1.1)
% Total canopy[b]	55.1^{B} (4.6)	84.3^{AC} (1.5)	57.2^{B} (5.3)	82.8^{C} (6.9)	61.2^{ABC} (2.2)
% Live canopy[b]	51.4^{A} (3.3)	74.6^{B} (1.6)	53.1^{AC} (5.6)	73.3^{BC} (5.6)	56.1^{AC} (2.3)
% Dead canopy[b]	3.9^{A} (0.9)	8.8^{B} (0.5)	4.6^{AB} (1.1)	9.4^{B} (1.6)	5.7^{AB} (0.7)
% Grass canopy[b]	26.9^{A} (4.2)	26.9^{A} (11.1)	45.4^{AB} (7.8)	53.8^{B} (2.6)	41.6^{AB} (3.0)
% Forb canopy[b]	29.1^{AB} (0.4)	54.8^{A} (10.6)	12.5^{B} (2.2)	28.4^{AB} (8.2)	20.7^{AB} (3.6)
% Woody canopy	0.0 (0.0)	0.8 (0.7)	<0.1 (<0.0)	0.0 (0.0)	0.2 (0.1)
% Litter cover[b]	25.6^{A} (12.2)	40.2^{A} (3.4)	57.5^{B} (3.8)	45.8^{AB} (1.4)	54.2^{AB} (1.9)
% Bare ground[b]	33.2^{A} (11.8)	7.1^{AB} (2.7)	2.5^{B} (1.6)	2.2^{B} (1.2)	2.5^{B} (0.7)
Litter depth (cm)[b]	2.3^{A} (0.9)	3.1^{AB} (1.8)	11.3^{B} (3.2)	6.7^{AB} (1.1)	5.6^{AB} (1.1)

[a] Five- and 6-year-old fields combined.

[b] Significantly different among age classes (Kruskal-Wallis, $P < 0.10$). Within the same row, means having the same letter are not significantly different (multiple comparison test, $\alpha = 0.10$. Miller 1980).

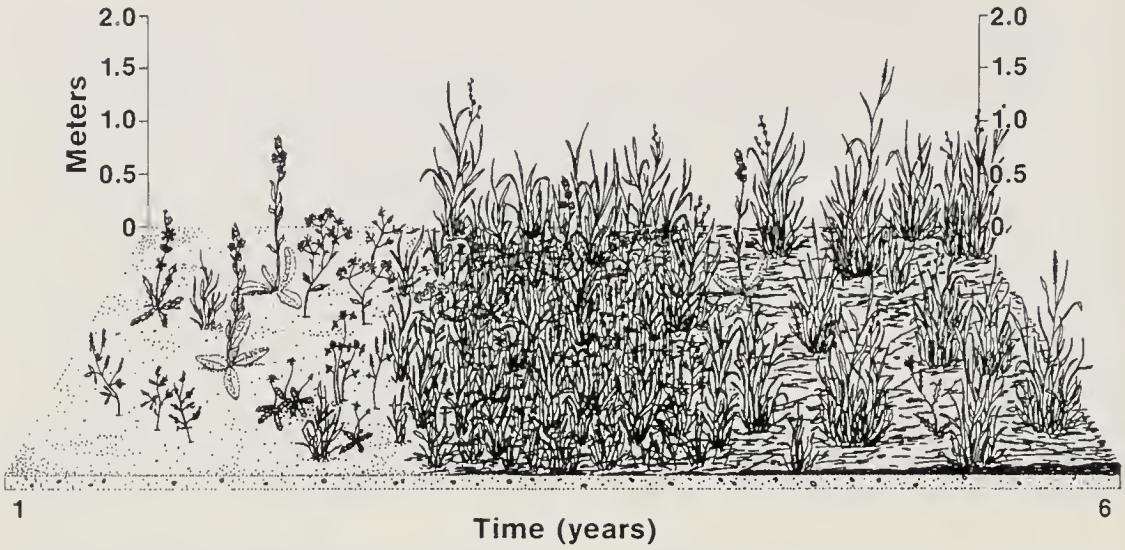

FIG. 1. Diagrammatic representation of changes in vegetation structure and composition on a Conservation Reserve Program field over the first six growing seasons.

field age. General patterns for horizontal cover, height of live and dead vegetation, percent total canopy, percent live canopy, percent dead canopy, and percent forb canopy suggest an increase (but not necessarily significantly) from 1- to 4-year-old fields, with the exception of a decrease in these variables during the third growing season (Fig. 1). These vegetation characteristics all decreased from the fourth to 5/6 growing seasons. Percent grass canopy increased through the fourth growing season, decreasing in the 5/6 growing season. Percent litter cover increased with field age, stabilizing after the third growing season. Litter depth was greatest during the third growing season, subsequently decreasing through the 5/6 growing season, whereas percent bare ground decreased from 1- to 5/6-year-old fields.

The first three principal components accounted for 81.5% of the variance in the vegetation variables (Fig. 2). Principal component one (PC 1), explaining 35.2% of the variance, represents a successional change in vegetation attributes from greater percent total and live canopy to greater percent litter cover and litter depth. Percent total canopy included percent live canopy and percent dead canopy but not percent litter cover. The second principal component (PC 2), explained 32.5% of the variance and represents a successional change from greater percent grass cover to greater percent forb cover. Principal component three (PC 3), explaining 13.7% of the variance, represents a successional change from greater percent bare ground to greater percent litter cover.

Thirty-two avian species were encountered on the CRP fields. The most common species encountered were Red-winged Blackbirds (*Agelaius*

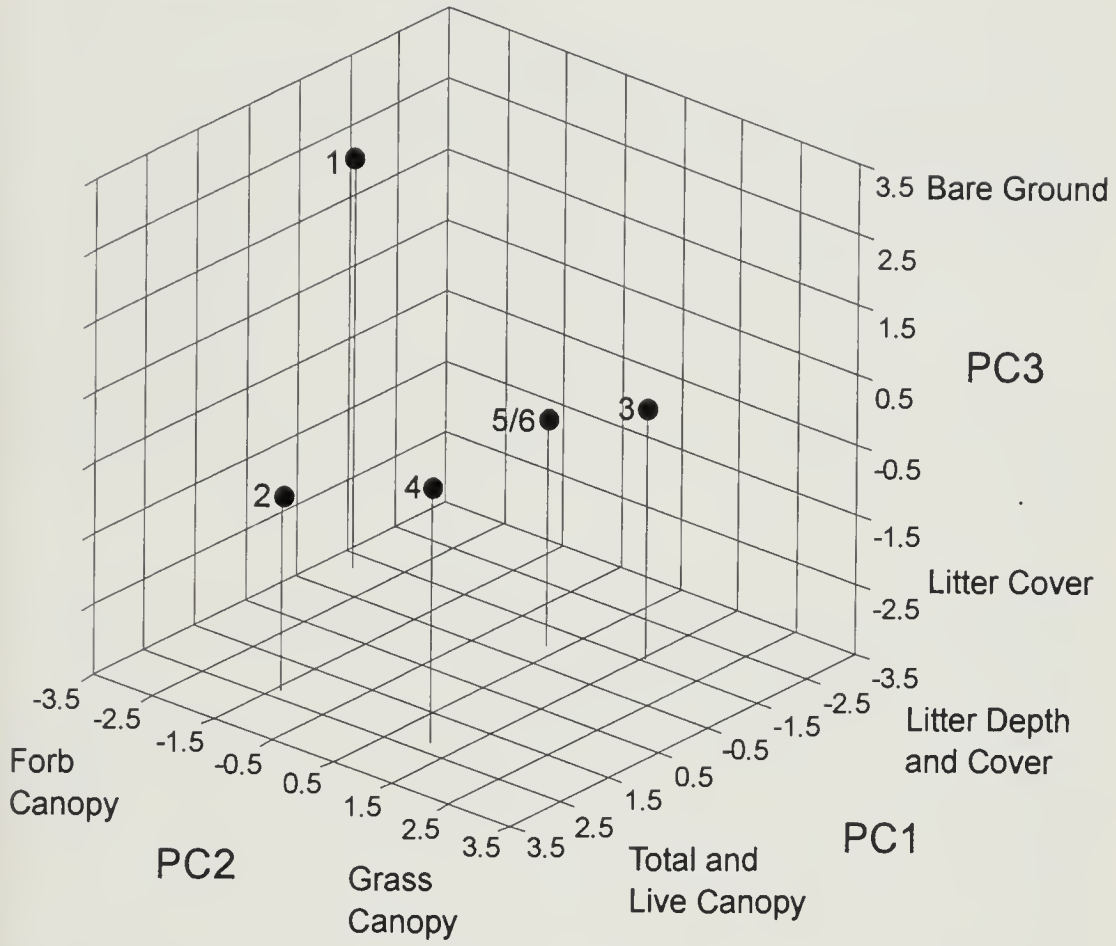

FIG. 2. Mean principal component (PC) values for the first three principal components for different age CRP fields. Age classes correspond to the appropriate number located at each point.

phoeniceus), Song Sparrows (*Melospiza melodia*), Bobolinks (*Dolichonyx oryzivorus*), and Sedge Wrens (*Cistothorus platensis*).

No differences (KW, $P > 0.10$) were detected in bird diversities within a census count among age classes. However, mean avian diversities were different (Friedman, $P = 0.04$) for the entire census period among age classes (Table 2), with 1-year-old fields having significantly greater diversities than 5/6-year-old fields.

Only the periods of 16–31 May and 1–15 August showed differences (KW, $P = 0.06$) in avian relative abundance among age classes, with 5/6-year-old fields having significantly lower relative abundance than 4-year-old fields for the period 1–15 August. However, a KW multiple comparison test did not detect differences among age classes for the period 16–31 May. Mean avian relative abundances were different for the entire census period among age classes (Friedman, $P = 0.01$; Table 2). Five/

TABLE 2

MEAN AVIAN RELATIVE ABUNDANCE (BIRDS/HA) AND DIVERSITY (SHANNON-WEAVER) ON DIFFERENT AGE CONSERVATION RESERVE PROGRAM (CRP) FIELDS[a]

Age class[b]	N	Relative abundance (SE)	Diversity (SE)
1	3	4.24 (1.01)^{AB}	1.37 (0.07^{A}
2	3	3.72 (0.63)^{AB}	1.36 (0.10)^{AB}
3	3	3.30 (0.50)^{AB}	1.28 (0.08)^{AB}
4	3	4.67 (0.57)^{A}	1.18 (0.04)^{AB}
5/6	7	2.12 (0.19)^{B}	1.15 (0.06)^{B}

[a] Within columns, means with the same letter are not significantly different (Friedman's multiple comparison, $\alpha = 0.10$, Miller 1980).

[b] Five- and 6-year-old fields combined.

six-year-old fields had significantly lower relative abundance than 4-year-old fields. Avian relative abundances decreased from 1- to 5/6-year-old fields with an increase on 4-year-old fields.

We found 166 active nests in three age classes of CRP fields. Nesting species monitored included Red-winged Blackbird, Vesper Sparrow (*Pooecetes gramineus*), Sedge Wren, Northern Harrier (*Circus cyaneus*), Mallard (*Anas platyrhynchos*), Ring-necked Pheasant (*Phasianus colchicus*), and unidentified sparrow species. Red-winged Blackbirds were the primary nesting species observed with 83.1% of the monitored nests.

No difference (KW, $P = 0.29$) was found in percent successful nests among 1-, 4-, and 5-year-old fields. However, nests on older fields (4- and 5-year-old) had greater probabilities ($\hat{S}_{Mayfield} = 0.283$ and 0.293, respectively) of surviving from initial egg laying to fledging than 1-year-old fields ($\hat{S}_{Mayfield} = 0.138$). Mean number of active nests (nests have at least one egg or young within the monitoring period) on 1-, 4-, and 5-year-old fields was 10, 22, and 23, respectively.

DISCUSSION

Although we could not distinguish age classes of CRP fields by the presence of particular dominant plant species (i.e., alfalfa, orchard grass), they could be described by gross structural characteristics (i.e., grass canopy, forb canopy). Fields in this study may be described as in a gradient from greater forb cover and bare ground in the youngest fields to greater grass and litter cover in the oldest (Fig. 1). Forb canopy cover was greater on younger fields due to initial seed mixtures and the natural invasion of other plant species, with many annual forbs responding to soil disturbance. Because of the recent disturbance of planting, bare ground was more dominant than litter cover on younger fields.

Two-year-old CRP fields, however, were best described by moderate forb canopy and litter cover, with a greater total/live canopy than bare ground (Fig. 1). Although the initial seed mixtures of younger CRP fields contained both alfalfa and orchard grass, orchard grass takes several years to establish, whereas alfalfa is noted for its quick establishment (J. Swanson, Gratiot County SCS, pers. commun.). Alfalfa, however, has a relatively short life cycle and begins to die out after two growing seasons. Total/live canopy would be greater on younger fields than litter cover/depth because a substantial litter layer has not yet developed. However, a litter layer was evident, and was proportionally greater than the amount of bare ground present.

Three-, 4-, and 5/6-year-old fields can be described by grass canopy and litter cover, with a decreasing total/live canopy (Fig. 1). As alfalfa begins to die back after the second growing season, grasses begin to dominate sites. The decline in forb cover after the first two growing season may be explained by the loss of alfalfa and other forbs and the encroachment of grasses. Basu et al. (1978) stated that vegetation on a legume dominated field undergoes successional changes, eventually becoming grass-dominated and sparser. As grasses began to dominate and out compete existing forb species, forb cover decreased. Also, as CRP fields age, a litter layer develops decreasing the amount of bare ground and serves as a mechanical barrier to grass development (Rice and Parenti 1978). This barrier decreases productivity of plants present, growth is isolated to surviving clumps, and total/live canopy cover becomes less dense.

It has long been accepted that vegetation structural complexity is associated with avian community structure (MacArthur and MacArthur 1961, Cody 1968). Typically, both avian species diversity and density increase with increasing habitat complexity (May 1982). This may only be expressed on established habitat types (i.e., forests, old fields) and may not be valid for newly established habitats (such as 1-year-old CRP fields).

Habitat complexity is likely not the primary or only factor affecting influx of birds onto 1-year-old CRP fields. Younger fields may meet a variety of habitat needs including feeding and nesting habitat not available on alternative vegetation types present in the landscape, such as agricultural fields. Although nesting did occur on younger CRP fields, productivity was less than that observed on older fields. Younger CRP fields may provide some suitable habitat for nesting, but it is likely that amount and quality of nesting habitat is limited. Roseberry and Klimstra (1984) reported that areas dominated by annual weeds (forb canopy) may provide

inferior nesting cover because of the lack of dead grass stems for nest construction.

Older CRP fields did not have the same high avian relative abundances as younger fields. Burger et al. (1990) suggested that CRP fields in Missouri do not provide quality nesting cover for Northern Bobwhites (*Colinus virginianus*) until the third year after establishment. Therefore, it may be possible that a greater quality and availability of nesting habitat was provided on older CRP fields in Michigan, thus supporting greater nesting compared to younger CRP fields.

Cody (1985) stated that avian species composition, or diversity, varies with vegetation structure following a disturbance, thereby creating a diverse array of avian species. Species diversity observed on CRP fields supports this. One-year-old CRP fields, newly disturbed by planting, supported the greatest diversity of avian species. As fields aged and became less disturbed diversities declined.

While many factors may be responsible for increasing avian productivity as fields age, this increase may be an artifact of the most dominant nesting species encountered, Red-winged Blackbirds which nest in a variety of locations with highly variable structural attributes (Granlund 1991). The conspicuous locations of Red-winged Blackbird nests allowed for easier detection. It is likely that nests of other species were missed due to the density of the vegetation. Results may only represent patterns in Red-Winged Blackbird nesting and not productivity of the entire CRP avian community.

Several studies have suggested that grasslands established with seed mixtures similar to planted CRP fields generally did not maintain structural qualities for more than seven years (Higgins et al. 1987). Disturbances on 3- to 5-year intervals enhance avian production by more than 100% (Kirsch 1974, Kirsch et al. 1978). There is general recognition (e.g., Schenck and Williamson 1991) that controlled, periodic treatments to revitalize cover by fire, grazing, or mowing may be necessary for the long-term maintenance of wildlife habitat in grassland ecosystems. Our results indicate perturbations may be necessary to maintain the greatest avian relative abundances, diversities, and productivity on CRP fields after 3–5 growing seasons. Further studies need to be completed to assess fully changes in vegetation attributes and avian diversity, relative abundance, and productivity on fields >6 years old.

Many types of disturbances such as mowing, burning, or discing may create the desired changes in the vegetation. Regardless of the form of perturbation, it should be accomplished in as short a period of time as possible and scheduled to minimize the disruptive effects to nesting wildlife. Although information is available on effects of disturbance practices

on grassland birds (e.g., Kirsch et al. 1978), CRP fields are a unique vegetation type in Michigan's agricultural landscape, and little is known about effects of disturbances on avian species using CRP fields. Additional information is needed on maintenance and rejuvenation methods for planted CRP grasslands and responses of avian species to these management practices.

ACKNOWLEDGMENTS

The Michigan Agricultural Experiment Station (NC-203 regional research project), Federal Aid in Wildlife Restoration Project W-127-R (administered by the Michigan Dept. of Natural Resources, Wildlife Division), Michigan Chapters of Pheasant Forever, and the Frank M. Chapman Foundation funded this study. Earlier versions of this manuscript were reviewed by L. Best, L. W. Burger, A. H. Farmer, and B. Leopold. Special thanks are extended to all cooperating landowners who allowed research to be conducted on their properties. Assistance in data collection was provided by interns S. Miller, J. DeDoes, and K. O'Brien and volunteers J. Fierke, M. Smith, and D. Hyde.

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Wilson Bull., 108(4), 1996, pp. 771–775

FEMALE BUNTINGS FROM HYBRIDIZING POPULATIONS PREFER CONSPECIFIC MALES

MYRON C. BAKER

ABSTRACT.—I captured five female Indigo Buntings (*Passerina cyanea*) and 12 female Lazuli Buntings (*P. amoena*) from a hybridizing population in Wyoming and tested them in the laboratory for their sexual display responsiveness to male traits (live male and broadcast vocalizations) of the two species. The females responded with more copulation solicitation displays when exposed to conspecific male traits than when exposed to heterospecific male traits. Consistent preference of female buntings for conspecific male characteristics in these choice tests, together with previous results, suggests that hybrid pairs may form when females are faced with a choice of mating heterospecifically or not at all. *Received 14 Nov. 1995, accepted 20 April 1996.*

Populations of Indigo Buntings (*Passerina cyanea*) and Lazuli Buntings (*P. amoena*) overlap and hybridize in the Great Plains of North America (Rising 1983). Although hybrids are easily found in some populations, mating is non-random with positive assortment being the general rule among the pure phenotypes of the two species (Emlen et al. 1975; Baker, unpubl. data). Non-random mating in the overlap populations could have a number of proximate explanations. Mate preferences could be established in allopatric populations and emigrants from these areas into sympatric populations may retain their preferences when encountering heterospecifics, at least in initial encounters. A previous experiment gave results consistent with this hypothesis (Baker and Baker 1990). On the other hand, continuing exposure of an immigrant female to the visual and vocal courtship displays of heterospecific males could perhaps alter her preferences. An extenuating circumstance might be the availability of male mates of the alternative phenotypes.

An earlier experiment (Baker 1994) exposed females from allopatry to heterospecific males during the time they were coming into reproductive condition upon photostimulation. This exposure was restricted to 25 days and occurred in cages in the laboratory. Such exposure to displaying males had no significant effect on female preference, as indicated by an assay of copulation solicitation displays, for conspecific males and vocalizations. It is likely that females in sympatric populations experience a longer and more intense level of exposure to heterospecific courtship than was achieved in the laboratory study, and this prolonged exposure might be effective in altering female preferences. If so, such altered preferences of females could lead to the formation of observed hybrid pair-

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ings. The present experiment was conducted to address the question of whether Lazuli and Indigo Bunting females from a natural population consisting of a mix of phenotypes have significant preferences for conspecific male traits when given a choice of conspecific versus heterospecific males and vocalizations in a controlled experiment.

METHODS

Seventeen female buntings (12 Lazuli, 5 Indigo) were captured in a hybridizing population in NE Wyoming. Captures were made 18–27 July 1989 of females with fully developed brood patches, indicating that they were reproductive. All the subjects were captured during the territorial period and all had both Lazuli and Indigo males in nearby territories. Some hybrid males also defended territories in the neighborhood. None of the birds was banded, however, so the identity of the mate was not certain.

The plumage characteristics of the females were evaluated by the criteria of Emlen et al. (1975). This character index judges three areas of female plumage: throat/breast, wing bars, and back/rump. A pure Indigo would score 0 in all three regions for a total score of 0, and a pure Lazuli would score 1 in all regions for a total score of 3. Intermediates in any region were given a score of 0.5. There was some subjectivity involved in applying the scoring system, so I considered scores of 0 and 0.5 as Indigo and of 2.5 and 3 as Lazuli.

The females were housed in separate cages in a single room in the laboratory. They were fed a seed mixture of canary grass and millet, turkey starter, vitamins, grit, and water. Starting 30 July, the photoperiod was gradually reduced to 8:16 (L:D) by 9 October and retained on this cycle until 22 January 1990 when the cycle was switched overnight to 16:8 (L:D). On 22 February, the females each received one silastic implant (10 mm long, 1.47 mm inside diameter, Dow Corning) subcutaneously in the breast region. Each implant contained 17-beta estradiol (Sigma Biochemical) and was sealed at both ends with silastic adhesive (Dow Corning). This treatment is necessary to bring females into full reproductive readiness in the laboratory.

Starting 5 February, each subject in her home cage was habituated to testing circumstances by being placed in an experimental chamber containing an empty cage and a loudspeaker. An observation booth one meter away was equipped with a video camera, one-way glass, and a cassette recorder for playing stimulus tapes over the loudspeaker. Each female had nine habituation sessions of 30 min at a rate of one session every other day.

In the experiment, a test session consisted of placing a caged female into the observation chamber together with a stimulus male occupying the adjacent cage and playing vocalizations, matched with his species, from the loudspeaker located on the side of the male cage away from the female. Previous studies indicated that both male plumage characteristics and vocalizations play significant roles in the expression of female preference as indicated by the copulation display assay. Four Lazuli and two Indigo males were used as stimuli. All were captured in allopatric populations and maintained together in acoustic isolation from the females. The males did not vocalize during female testing, although they hopped around in the cage. Following 3 min of initial silence, the loudspeaker broadcast a sequence of 1 min of male songs at a rate of one song each 15 sec, 1 min of "tseep" calls (a courtship call, Thompson and Rice 1970, Thompson 1976) at a rate of one tsecp every 10 sec, 1 min of male songs (different from those in the first min), 1 min of "tseep" calls, 1 min of male songs (also different from the earlier songs), and a final minute of "tseep" calls. The "tseep" call, similar in the two species, is an important component of courtship vocal behavior and increases female responsiveness in the laboratory assay (Baker and Baker 1988).

From 3–12 March, half the females were tested first with Lazuli males and vocalizations

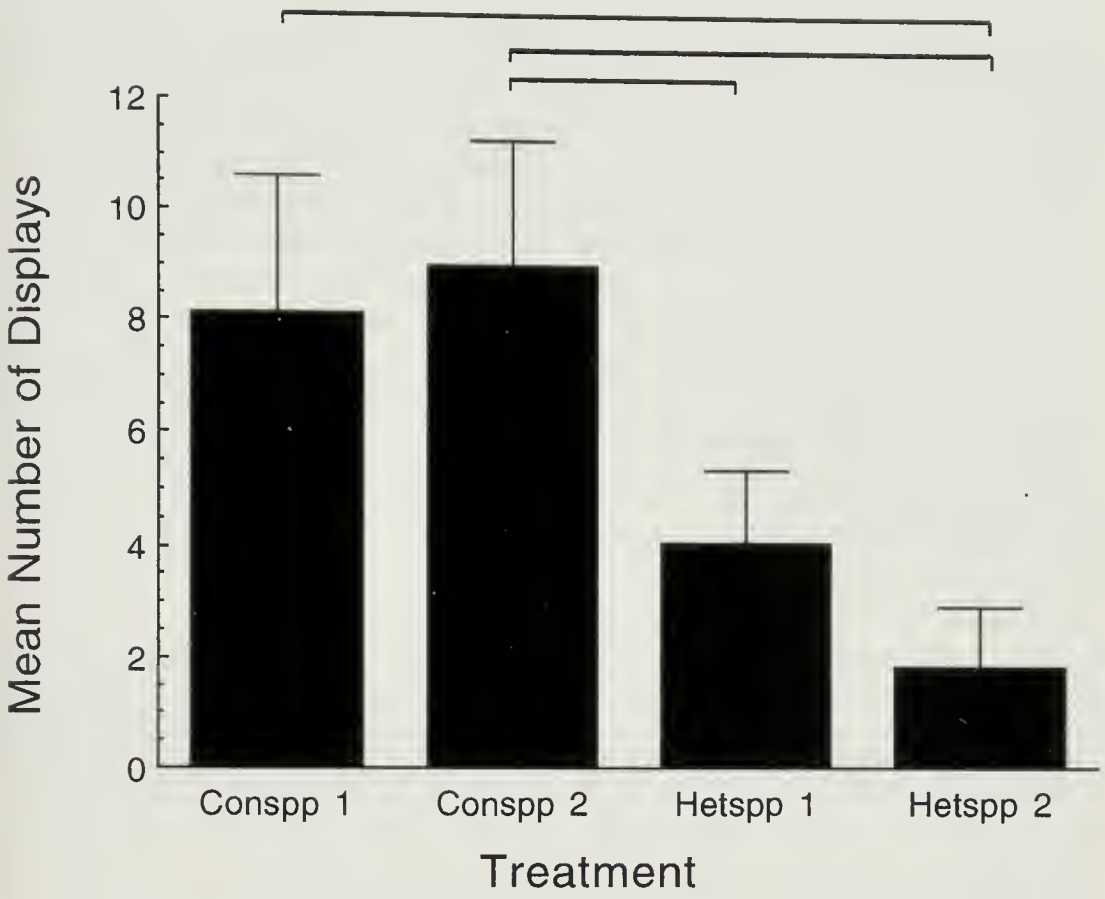

FIG. 1. Mean number of copulation solicitation displays (+1 SEM) elicited from female buntings by conspecific versus heterospecific males and their recorded vocalizations. Horizontal lines above histogram bars connect pairs of treatments that were significantly different.

and then with Indigo males and vocalizations. The other half the females were tested with the order of stimuli reversed. No subject was tested twice on the same day, and there was at least 1–2 days between successive tests on a female. With completion of these first test sessions, the stimulation of the subjects by conspecific stimuli was considered one treatment, and the stimulation by heterospecific stimuli was considered a second treatment. A second set of tests followed the first and again presented Lazuli and Indigo stimuli to each subject. In this set, the stimulus male presented to each female differed from the one she had experienced in the first set, and an entirely new group of songs was used for the vocal stimuli. The same tseep calls were used, however, because of a paucity of good quality recordings of this vocalization. With completion of this second set of tests, presentation of conspecific stimuli constituted a third treatment and presentation of heterospecific stimuli a fourth treatment. I used repeated measures ANOVA and Fisher's LSD for multiple comparisons (Winer 1971) for statistical analyses.

RESULTS

In the treatments involving exposure to conspecific males and vocalizations, the females exhibited a high level of responsiveness (Fig. 1). The

average number of copulation solicitation displays elicited by the first conspecific treatment (Conspp-1) was 8.1 and that by the second conspecific treatment (Conspp-2) was 9.0 (ns, $P > 0.05$, Fisher's LSD). The two treatments presenting heterospecific males and vocalizations elicited lower numbers of solicitation displays (Fig. 1). The average number of displays elicited by the first heterospecific treatment (hetspp-1) was 4.0 and by the second heterospecific treatment (hetspp-2) was 1.8 (ns, $P > 0.05$, Fisher's LSD).

In comparing conspecific to heterospecific treatments, the number of solicitation displays elicited by both Conspp-1 and Conspp-2 were greater than the number elicited by Hetspp-2, and the number elicited by Conspp-2 was greater than that elicited by Hetspp-1 (Fig. 1, all Ps < 0.05, Fisher's LSD). The comparison between Conspp-1 and Hetspp-1 did not give a significant difference.

Comparing responses of Indigo (N = 5) and Lazuli (N = 12) females within each treatment revealed that there were no differences in display production in three of the four treatments (Conspp-1, $P = 0.36$; Conspp-2, $P = 0.45$; Hetspp-1, $P = 0.70$; Mann-Whitney U-tests, two tailed, Siegel 1956). In the Hetspp-2 treatment, however, Indigo females averaged more displays than Lazuli females ($P = 0.01$, Mann-Whitney U-test, two tailed). In this treatment, only two of the 12 Lazuli females gave displays whereas four of the five Indigo females gave displays.

DISCUSSION

The results suggest that prolonged exposure of females to the songs and plumages of both Indigo and Lazuli bunting males in a natural breeding association does not alter preference for conspecific traits. Although the exact nature of previous experience of each female is unknown, it is possible to outline the range of possible exposures the subjects had prior to testing. These migrants arrived in the study area in late May and early June. In the immediate neighborhoods of the subjects were territorial Lazuli, Indigo, and hybrid males. Given capture in late July, it is likely that the females were exposed to males of all three types for a minimum of 5–8 weeks. Alternatively, any or all of the subjects could have hatched in a mixed population and experienced one or more breeding seasons in such a context. Thus, the experience the females had with males and songs prior to testing occurred in a natural population and was probably more intense and longer than was provided in the earlier laboratory experiment that attempted to alter adult female preferences (Baker 1994). Although the experimental females were relatively refractory to the potentially influential presence of alternative species' male phenotypes, it is possible

that more extreme amounts of exposure could affect changes in female preference.

The general inference that can be made from these results is that when given a choice between conspecific and heterospecific males and vocalizations, female buntings prefer conspecific male traits. This implies further that heterospecific pairings in natural populations may result from females making the best of a bad job, choosing to mate heterospecifically rather than not mate at all. A female with a territory retains the possible option of extra-pair fertilization (Westneat 1990) with neighboring conspecifics while having the benefit of a nest site, feeding area, and other advantages of territorial residence. A similar pattern of female behavior has been observed in Fairy-Wrens (*Malurus splendens*), (Brooker and Rowley 1995), in which social pairing by a female appears to allow the opportunity for matings with high quality neighboring males.

ACKNOWLEDGMENTS

Chris Goulart and Jean Boylan assisted with the fieldwork and with maintenance of the captive birds. Capture was authorized by state and federal permits (Wyoming 1989-16, Federal PRT-694924). Financial support was from the National Science Foundation (BNS-87-06526). Helpful comments were received from David Westneat and an anonymous reviewer.

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Wilson Bull., 108(4), 1996, pp. 776–782

SURVEYS OF PUERTO RICAN SCREECH-OWL POPULATIONS IN LARGE-TRACT AND FRAGMENTED FOREST HABITATS

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ABSTRACT.—We conducted road surveys of Puerto Rican Screech-Owls (*Otus nudipes*) by playing conspecific vocalizations in secondary wet forest and fragmented secondary moist forest in rural areas of eastern Puerto Rico. Six paired surveys were conducted bi-weekly beginning in April. We recorded number of owl responses, cloud cover, wind speed, moon phase, and number of cars passing during 5-min stops at 60 locations. Owls responded in similar numbers ($P > 0.05$) in both habitat types. Also, we detected no correlation of the number of owls with cloud cover, wind speed, moon phase, or passing cars. *Received 29 Dec. 1995, accepted 15 May 1996.*

The endemic Puerto Rican Screech-Owl (*Otus nudipes*) is common throughout forested areas of mainland Puerto Rico but is thought to be extirpated on adjacent islands such as Culebra and Vieques (Raffaele 1989). Although Puerto Rican Screech-Owl populations may have declined in the early 1900s when many of the islands' forests were cleared (Wiley 1986a), Wiley (1986b) reports that the owl population recovered as forest cover increased and as trees grew large enough to provide suitable nesting and roosting cavities.

Unfortunately, Puerto Rican Screech-Owl populations have seldom been studied (Recher 1970, Snyder et al. 1987, Rivera-Milán 1995). Since Eastern Screech-Owl (*Otus asio*) abundance is positively correlated with amount of woodland habitat available (Nowicki 1974, Cink 1975, Smith et al. 1987), we hypothesized that Puerto Rican Screech-Owls occupy fragmented forests at lower densities, if at all. Our objective was to determine the relative abundance of owls in fragmented and large forests of eastern Puerto Rico.

METHODS

Study areas (each ~2500 ha) were in secondary subtropical wet forest (large tract) of the Luquillo Mountains at elevations from 90–455 m and in secondary subtropical moist forest

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(fragmented) near Naguabo, Puerto Rico (18°18′N, 65°30′W), at elevations from 22–224 m (Ewel and Whitmore 1973). The forests receive 233–392 cm of rainfall annually and have an average temperature of 25°C (Brown et al. 1983).

Percent cover of general habitat types was visually estimated by two observers to the nearest 10% within approximately 300 m of each owl survey point. Average percent cover in large-tract forest was 80% intermediate forest, 15% young forest, 4% scrub (storm blow-down areas), and 1% residential. Average percent cover at survey points in the fragmented forest was 27% intermediate forest, 9% young forest, 19% scrub, 34% pasture, and 11% residential.

To estimate relative owl populations, we conducted road surveys using vocalization playback to elicit owl responses. In each study area (12 km apart), we established three 3.6-km road surveys with 10 points per survey site (points 0.4 km apart). Distance between survey points was determined by research in the summer of 1990 and from home ranges determined for two radio-marked Puerto Rican Screech-Owls (Gannon et al. 1993). Roads with heavy traffic (>3 cars per 5-min point count) at night were avoided. Survey sites were selected by lottery from suitable roads (no heavy traffic) near Naguabo (Highway 971, 972, and 974) and in the Luquillo Mountains (Highway 988, 9966, and 191). Survey sites were paired between study areas, i.e., paired points were sampled simultaneously throughout the study.

We conducted six surveys during the owls' 1991 breeding season—five biweekly surveys beginning in late April and one in July. Surveys began 30 min after sunset (about 19:20) and ended about midnight. We randomly selected the survey order and rotated the order on subsequent samplings so that each point was sampled twice during early (19:20–21:00), mid- (21:00–22:30), and late evening (22:30–24:00).

At each point, we conducted a 5-min survey consisting of visual and aural observations. Playback overlapped the first 2 min of observation and was followed by 3 min of silence. The first minute of playback consisted of 30 sec of owl trills followed by 30 sec of "wild" trills or cackles (van der Weyden 1974). This sequence was repeated during the second minute after turning the speaker to the opposite direction and perpendicular to the edge of the road. We used Marantz® (model PMD 430) and Sony® (model TCM-5000EV) cassette recorders with amplified external speakers (Realistic® Minimus-0.6, 2 W) to broadcast owl calls. (Use of brand names does not constitute government endorsement.) Speaker volumes were equal and audible to us to 160 m. To test observer variability, two persons recorded owl responses independently and simultaneously at each point in the large-tract forest. Both observers were equally trained and experienced (Kepler and Scott 1981). At each point we recorded (1) number of initial owl responses within 5, 1-min periods, (2) cloud cover (nearest 10%), (3) wind speed (Beaufort scale), (4) moon phase, and (5) number of cars passing the point in 5 min.

We analyzed the data with *t*-tests (SAS Institute, Inc. 1988) that compared the mean differences ($\bar{d}$) of variables between paired points. Differences were considered significant at $P \leq 0.05$. Pearson correlation analysis (SAS Institute, Inc. 1988) was used to determine associations between number of owl responses with wind speed, moon phase, cloud cover, and number of cars. Weather conditions were different between the study areas during the surveys. More cloud cover ($\bar{d}$ = 17%, P = 0.0001) and higher winds (Beaufort scale, $\bar{d}$ = 1.7, P = 0.0001) were present during surveys in large-tract forest. However, more cars ($\bar{d}$ = 0.8, P = 0.0001) were present during surveys in fragmented forest. Because of these differences the association of weather and number of cars with number of owl responses was analyzed separately for each study area. Data were normalized using the square root of x (x = cloud cover and wind speed) and the square root of [y + 0.5] (y = number of owls, moon phase, and number of cars) transformations.

RESULTS

Paired mean difference ($\bar{d}$) of owl responses by study areas was not different from 0 ($P = 0.53$) among survey dates; therefore, data for all dates were pooled. No differences in owl responses were found between study areas ($P = 0.31$). In the large-tract forest, a total of 200 owl responses ($\bar{x} = 1.10$ per point per survey) was found compared to 173 owl responses ($\bar{x} = 0.96$ per point per survey) in fragmented forest (Table 1). Observers conducting simultaneous point surveys for owls in large tract forest did not detect owls in different numbers (overall $\bar{x}$ for observer 1 = 1.11 owls/point and $\bar{x}$ for observer 2 = 1.15 owls/point, $P = 0.60$). Cloud cover, wind speed, and number of cars were not associated with number of vocal responses of owls at either study area (r ranged from −0.054 to 0.12 and P from 0.12 to 0.97). In large-tract forest, the number of vocal responses of owls was weakly correlated with moon phase ($r = 0.15$, $P = 0.04$). No correlation was found between moon phase and number of vocal responses by owls in fragmented forest ($r = 0.08$, $P = 0.22$). Of a total of 373 aural and visual responses, 18.5% were recorded in the first minute, 4.8% in the second, 31.6% in the third, 22.0% in the fourth, and 23.1% in the fifth. Only, 4.8% of total contacts were visual, all occurring after the first survey minute.

DISCUSSION

Puerto Rican Screech-Owls responded similarly in fragmented habitat (36% forest cover) and large tract habitat (95% forest cover) which may indicate similar owl densities. This is contrary to studies on Eastern Screech-Owls in Michigan (Nowicki 1974) and Kansas (Cink 1975) which indicated that abundance was positively associated with forested habitat. Similar numbers of owls in fragmented and large-tract forests suggests that restoration of the Puerto Rican Screech-Owl may be possible in former ranges where forest habitat is fragmented (e.g., Vieques Island) but where nesting cavities (artificial or natural) and food resources are adequate.

Traditionally, the Vieques owl population has been listed as the *O. n. newtoni* subspecies (Bond 1956). However, lack of a specimen from Vieques and the paucity of information, in general, on the Puerto Rican Screech-Owl indicate that owls on this island were part of the geographically closer and more abundant race, *O. n. nudipes* (R. Banks, pers. commun.; J. Marshall, pers. commun.). In addition, there is some uncertainty as to the existence of two separate owl races (R. Banks, pers. commun.; Biaggi 1970). No attempts to introduce owls from Puerto Rico to the Virgin Islands should be undertaken while this species taxonomic status is in question.

TABLE 1

NUMBER OF PUERTO RICAN SCREECH-OWLS AND MEAN DIFFERENCE ($\bar{D}$) BETWEEN UNFRAGMENTED TROPICAL WET FOREST AND FRAGMENTED TROPICAL MOIST FOREST

Total number of owls[a]		
Unfragmented forest	Fragmented forest	$\bar{d}$
7	3	0.67[b]
5	3	0.33
11	7	0.67
6	7	−0.17
9	7	0.50
4	11	−1.17
11	1	1.67
5	4	−0.17
9	4	0.83
2	8	−1.00
8	5	0.33
11	7	0.67
10	7	0.50
6	5	0.17
3	3	0.00
10	2	1.33
6	8	−0.33
11	0	1.83
4	3	0.17
8	2	1.00
5	4	0.17
3	4	−0.17
2	2	0.00
10	17	−1.17
5	9	−0.67
5	3	0.33
12	4	1.33
1	8	−1.17
10	11	−0.17
1	14	−2.17
Total 200	173	

[a] Total number for six surveys of 5 min each.

[b] Mean difference per point per survey; paired t-test of mean difference (owls counted for point by survey for unfragmented forest minus owls counted for point by survey for fragmented forest) of transformed data is $t = 1.31$, df = 29, $P = 0.20$.

Future research, prior to screech-owl restoration efforts, should include surveys of former and current ranges to assess (1) the status of extant owl populations, (2) the availability of nesting and roosting cavities, and (3) the availability of food resources. Since these owls readily use nest

boxes, otherwise suitable habitat can be supplemented with artificial cavities (Wiley 1985, 1986a). Our data further suggests that Puerto Rican Screech-Owls may be able to exist in moist and wet areas with fragmented forest cover of approximately 36%. But the extent to which Puerto Rican Screech-Owls use fragmented forest must also be determined. Is fragmented forest preferred owl habitat or does it serve only as a population sink for individuals dispersing from large-tract areas?

Smith et al. (1987) and Gerhardt (1991) reported that Eastern Screech-Owl and Mottled Owl (*Ciccaba virgata*) responses were negatively associated with wind speed, whereas Carpenter (1987) suggested that subzero temperatures had inhibitory effect on Eastern Screech-Owl calling. Unlike Eastern Screech-Owls (Smith et al. 1987, Ritchison et al. 1988, Carpenter 1987) and Mottled Owls (Gerhardt 1991), Puerto Rican Screech-Owl responses may be weakly associated with moonlight. This weak association was probably caused by the absence of full and new moon phases during our sampling periods. In Puerto Rico, the lack of association of owl responses to all weather conditions discussed above, except moonlight, may be related to the mild temperature fluctuations of the tropical environment.

Puerto Rican Screech-Owls responded well to conspecific vocalization playback, with contacts occurring throughout the 5-min period. However, the lower numbers of responses in the first 2 min suggests that playback may interfere with the observers aural detection ability. In addition, after a 5-min survey, the accumulated number of initial owl responses had not stabilized. Therefore, five minutes per point may not be long enough to provide data for quantitative estimates of the owl population. Some studies suggest at least a 10-min sample period when surveying Eastern Screech-Owls and other raptors, especially when trying to determine population densities (Mosher et al. 1990, De Geus and Bowles 1991).

ACKNOWLEDGMENTS

We thank P. Pagán and N. López for their kind support and use of their vehicle. We are also grateful for the helpful comments provided by reviewers W. J. Arendt, C. Henny, D. G. Smith, R. B. Waide, and J. W. Wiley. We thank the U.S. Dept. of Agriculture Forest Service for providing access to study areas in the Caribbean National Forest. In addition, we are indebted to the U.S. Dept. of Interior, National Biological Service, for the use of field and office equipment throughout the study.

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Wilson Bull., 108(4), 1996, pp. 783–796

THE USE OF COASTAL AGRICULTURAL FIELDS IN VIRGINIA AS FORAGING HABITAT BY SHOREBIRDS

STEPHEN C. ROTTENBORN

ABSTRACT.—I studied temporal abundance patterns and use of cover types by shorebirds foraging in coastal croplands on the eastern shore of Virginia from March 1991 through February 1992. A total of 21,254 shorebirds of 21 species was observed foraging in agricultural croplands. Shorebird abundance reached a peak during spring migration and was lower during fall and winter. Shorebird species richness was highest in fall and lower in spring and winter. Some species appeared to use fields primarily as alternate foraging habitat when preferred intertidal habitats were covered by high tides, whereas other species foraged in fields regardless of tidal height. Most species showed highly significant positive associations with plowed fields (bare earth) and negative associations with herbaceous vegetation >10 cm tall. Associations with vegetated cover of <10 cm varied seasonally, tending to be positive in spring and negative (or with no association) in fall and winter for most species. Because most shorebirds foraged on the cover type providing the least cover from predators (plowed fields), the observed cover associations may reflect differences in predator detection or foraging efficiency among the cover types. *Received 20 Nov. 1995, accepted 13 April 1996.*

Most research on habitat use and foraging strategies of shorebirds has focused on the use of intertidal habitats, where they may choose different foraging sites and strategies depending on tidal conditions (cf Burger et al. 1977, Connors et al. 1981). When preferred intertidal habitats are inundated by high tides, shorebirds may forage temporarily in alternate areas, including agricultural fields (Atkinson 1976, Gerstenberg 1979, Page et al. 1979). Previous studies of the use of agricultural croplands by shorebirds have dealt primarily with species that prefer upland habitats and rarely move to intertidal areas (Fuller and Youngman 1979, Barnard and Thompson 1985, Milsom et al. 1985) or were conducted in inland regions where tidal regime had no influence on shorebird distribution and behavior (Ohmart et al. 1985). In California, a number of shorebird species move from intertidal areas to pastures during high tides (Gerstenberg 1979, Page et al. 1979), and some of the habitat features associated with the birds' use of coastal pastures have been described (Colwell and Dodd 1995). Despite the potential importance of cropland as alternate foraging habitat for shorebirds (Ohmart et al. 1985), the use of coastal cropland by foraging shorebirds has not been described. The objectives of this study were (1) to determine the species composition and temporal abundance patterns of shorebirds foraging in coastal cropland on the Eastern

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Shore of Virginia, and (2) to determine patterns of cover use by these shorebirds.

STUDY AREA AND METHODS

I conducted this study on the southern tip of the Eastern Shore of Virginia, within an area of approximately of 170 km^2. The study area is bounded to the east by extensive tidal salt marsh, mud flats, and barrier islands and to the west by narrow sandy beaches (with several tidal creeks) along Chesapeake Bay. Large numbers of shorebirds forage in these tidal areas, especially at low tide when beaches and mudflats are exposed. Previous observations indicated that individuals of some shorebird species moved from these intertidal habitats to agricultural croplands to forage during high tide.

In order to determine the relationship between tidal height and the abundance of certain shorebird species in agricultural fields, I conducted four surveys of a small number of fields in the study area (6–8 fields/survey). The days on which these censuses were conducted, 29 May, 12 and 31 August, and 2 November 1991, were chosen so that the timing of high and low tides varied among surveys. Such variation in the timing of high and low tides allowed me to distinguish possible relationships between shorebird abundance and time of day from relationships between shorebird abundance and tidal height. During these surveys, I visited each field at one- to two-h intervals between dawn and dusk, recording the number of individuals of each species in each field during each round of censuses. All fields were visited the same number of times on a given date, but the number of census rounds varied from seven to nine among different survey dates. I divided the species observed in fields into two groups based on my previous experience with shorebirds in intertidal habitats around the study area and life history information (Stout 1967, Hayman et al. 1986): field specialists, thought to forage primarily in fields and rarely visiting intertidal habitats, and field exploiters, species that regularly forage in intertidal habitats during low tide but occasionally forage in fields during high tide. For each field, the abundance of shorebirds in each of these groups was determined for the censuses conducted closest to the times corresponding to high and low tide at Cape Charles, Virginia (U.S. Department of Commerce 1990). Paired comparisons *t*-tests were used to test the null hypothesis that the abundance of shorebirds in these fields did not differ between high tide and low tide (Sokal and Rohlf 1981).

In order to determine seasonal patterns of shorebird abundance and the use of various cover types by shorebirds foraging in coastal croplands, I conducted thirty censuses of croplands (comprising 4598.8 ha) in the study area from March 1991 through February 1992. For the purpose of determining the relative availability of cover types, I defined a field as a continuous plot with homogeneous cover of bare earth or herbaceous vegetation of the same height class (<10 cm or >10 cm) not divided by a paved road or by woody vegetation. Because high and low tides were separated by approximately 6.0–6.5 h, I began each census 4 h before high tide so that all fields would be surveyed during the highest 2/3 of the tidal cycle. Each census lasted approximately 8 h. To randomize the tide height during my observation of any particular field, I began each census at a location chosen randomly from a pool of 20 points along the census route. Censuses were not conducted if visibility was hampered by fog or precipitation.

During each census, I drove along the census route, stopping at each field to scan for shorebirds. I counted shorebirds from one or more points at the edge of each field using 8.5× binoculars. For larger fields and for fields with taller vegetation, I scanned from several points along the edge of each field, using a 22× spotting scope as necessary. Scanning along rows of vegetation and listening for the birds' calls (given frequently by foraging flocks)

aided in the detection of shorebirds. For large or widely dispersed flocks, I made replicate counts of shorebirds and recorded the mean of the original and replicate counts. Most of the shorebirds observed on croplands were actively foraging, with only a small proportion roosting. Observations made during the four dawn-to-dusk surveys and at other times suggested that very few shorebirds, if any, used these fields for roosting without spending some time foraging. Therefore, all shorebirds recorded during censuses were assumed to be foraging in the fields.

I was able to corroborate the accuracy of counts for cover types of <10 cm vegetation and plowed fields by locating three fields with each of these cover types that contained large flocks of foraging shorebirds, counting the birds from the edge of each field, and then walking through the fields to flush and count every bird. In all six cases, the error in these replicate counts was less than two percent. I was unable to corroborate directly my counts for >10 cm cover, but on one occasion a disturbance in a field of tall vegetation flushed the shorebirds within the field, confirming my previous count.

During each census, I recorded the type and height of cover in each field. I recognized three cover types in these croplands: plowed (bare earth with no vegetation), herbaceous vegetation <10 cm tall, and herbaceous vegetation >10 cm tall. No distinction was made between row crops (which included cotton, soybeans, potatoes, string beans, and several other crops) and mat crops (mostly cereals). Fields with weedy herbaceous vegetation allowed to grow in the interval between the harvest of one crop and seeding of another were also included in this study, although I excluded fields that lay fallow for the entire study period. All crop types reached heights exceeding 10 cm, so vegetation height (<10 cm or >10 cm) was not dependent on crop type. I did not include any pastureland in this study, as very little was present within the study area.

The area of each field was measured with a planimeter from field-checked 7.5-min topographic maps. For each census, I summed the areas of all fields with a particular cover type to determine the total availability of each cover type in the study area. I then determined, for each census, the number of individuals of each shorebird species expected to occur in fields with each cover type if shorebird distribution over the study area were independent of cover type. These numbers were the products of the total number of observed individuals of each species and the proportion of fields having each of the three cover types. I summed the numbers of shorebirds observed and expected on each cover type over all censuses in each season in order to determine the total number of individuals of each species that were observed and expected on each cover type by season. In pooling these numbers by season, I assumed that patterns of cover use did not differ significantly among different censuses within the same season.

For the purposes of this study, I delimited seasons a posteriori by examining abundance patterns of species known to occur in coastal Virginia as summer or winter residents or as northbound (spring) or southbound (fall) migrants (Kain 1987). I defined summer as the period from early June until mid-July, during which the only species observed in the study area was a local breeder. Fall lasted from the arrival of the first southbound migrants in late July until the departure of the last southbound transients (i.e., species that do not overwinter in Virginia) from the study area in mid-November. Winter extended from mid-November until late March. Spring began with the first arrival of northbound migrants in early April and ended in late May. Because I observed only two individuals of one locally breeding species during summer, analyses presented here are restricted to fall, winter, and spring. Sampling intensity differed among seasons due to differences in season length; four censuses were conducted during summer, 10 during fall, 11 during winter, and five during spring.

For the species represented by at least 30 individuals during a given season, I used a χ^2 test to test the null hypothesis that shorebird distribution was independent of cover type. I

performed these χ^2 tests separately for each season. In a few cases, the expected number of individuals on both plowed and <10 cm vegetation was less than five; in such cases, the numbers of shorebirds observed and expected were pooled for these cover types, allowing for a valid test (Sokal and Rohlf 1981). Each total χ^2 value was the sum of three "component χ^2" values, one for each of the three cover types. If the total χ^2 exceeded the critical value (rejecting the null hypothesis), then each "component χ^2" was examined individually to determine which of the shorebird-cover associations were significant. If a "component χ^2" for a single cover type was so high that it exceeded the critical χ^2 value required for significance for the entire test, then the association between the species and the cover type in question was deemed significant. This method provided a conservative approach to assessing individual species-cover associations. The nature of each significant association was identified by determining whether the number of individuals observed on a cover type was greater than or less than the number expected on that cover type (indicating a positive or negative association, respectively).

Standard χ^2 tests assume independence of individuals, an assumption that may be violated in species, such as shorebirds, that frequently move in flocks. In this study, I was rarely able to determine the number of independent groups of shorebirds that selected a field for foraging. However, to treat the entire shorebird assemblage in each field as a single unit composed of interdependent individuals may unnecessarily reduce the number of observations available for analysis if, indeed, the shorebirds individually display their own cover preferences. In order to determine whether cover use may have been affected by social interactions, I examined the results of the χ^2 tests a posteriori. If flocking, rather than selection of a desired cover type, had been the primary influence on the birds' choice of fields, I would have expected a preponderance of insignificant, weak, or inconsistent shorebird-cover associations. However, the consistent, strong cover associations observed in this study indicate that social interactions did not mask actual patterns of cover preference or avoidance, supporting the validity of the χ^2 tests as they were conducted. I conducted an analysis of variance (in SYSTAT, Wilkinson 1990) to test the null hypotheses that mean species richness and shorebird abundance per census did not differ among the seasons.

RESULTS

Relationship between shorebird abundance and tidal height.—During the four dawn-to-dusk surveys, those species thought to prefer foraging in intertidal habitats (field exploiters) were most abundant on croplands during the higher portion of the tidal cycle and were scarce or absent during the lower portion (Fig. 1). During these surveys, such species included Semipalmated Plover, Black-bellied Plover, Whimbrel, Willet, Ruddy Turnstone, Semipalmated Sandpiper, Least Sandpiper, and Dunlin (scientific names in Table 1). Abundance of these shorebirds in fields at high tide and low was significantly higher during censuses conducted near high tide on 29 May ($t = 2.670$, df = 5, $P < 0.05$), 12 August ($t = 3.940$, df = 6, $P < 0.01$), 31 August ($t = 4.255$, df = 7, $P < 0.01$), and 2 November ($t = 2.449$, df = 6, $P < 0.05$). According to Fig. 1, relatively few field exploiters were present on censuses conducted more than two hours preceding or following high tide, although peak abundance did not always coincide with the census conducted nearest high tide (e.g., 29 May). Peak shorebird abundance occurred at different times during the

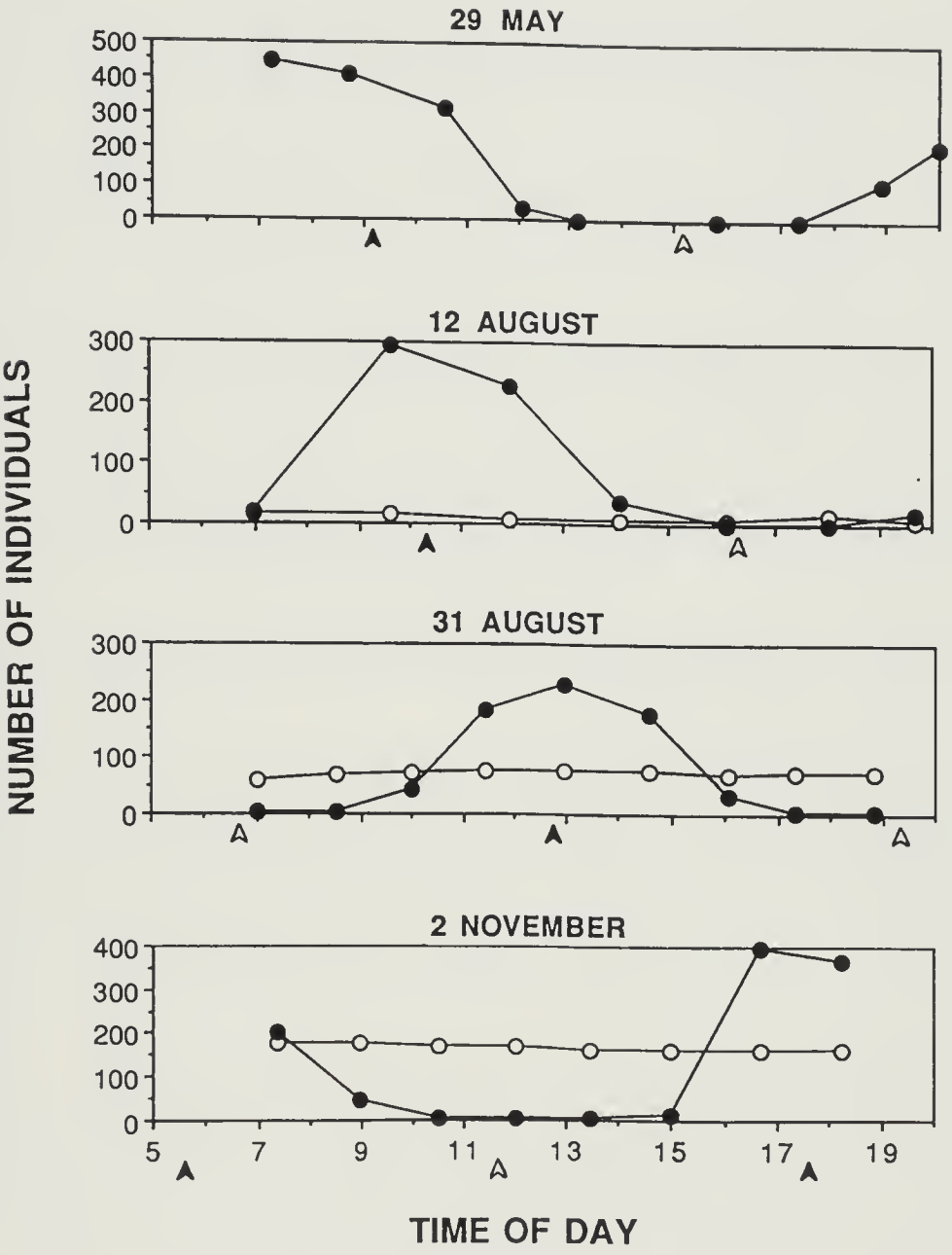

FIG. 1. Plots of shorebird abundance vs time of day. Solid circles represent individuals of "field exploiter" species, while open circles represent "field specialist" species (see "Methods" for descriptions of these two groups). Labels on the lower axis indicate hours after midnight. Solid and open arrows along the lower axis signify the times of high and low tides, respectively.

different surveys, indicating that these dynamics were related to tidal height and not time of day.

In contrast, the abundance of species thought to forage almost exclusively in fields (field specialists), including Killdeer, American Golden-

TABLE 1

ABUNDANCE OF SHOREBIRDS FORAGING IN AGRICULTURAL FIELDS BY SPECIES AND SEASON

Species	No. of censuses	No. of individuals	Percent of total	No. of individuals/season		
				Spring (N = 5)[a]	Fall (N = 10)	Winter (N = 11)
Black-bellied Plover (*Pluvialis squatarola*)	20	7982	37.6	4664	2033	1285
Dunlin (*Calidris alpina*)	15	6911	32.5	3252	959	2700
Semipalmated Plover (*Charadrius semipalmatus*)	14	4121	19.5	2822	1299	0
Killdeer (*C. vociferus*)	18	1039	4.9	1	869	169
Semipalmated Sandpiper (*Calidris pusilla*)	8	560	2.6	502	58	0
Short-billed Dowitcher (*Limnodromus griseus*)	9	233	1.1	138	53	42
Pectoral Sandpiper (*Calidris melanotos*)	6	90	0.4	0	90	0
Willet (*Catoptrophorus semipalmatus*)	6	68	0.3	68	0	0
Ruddy Turnstone (*Arenaria interpres*)	6	64	0.3	51	13	0
American Golden-Plover (*Pluvialis dominica*)	9	57	0.3	0	57	0
Western Sandpiper (*Calidris mauri*)	6	37	0.2	0	34	3
Buff-breasted Sandpiper (*Tryngites subruficollis*)	4	31	0.1	0	31	0
Upland Sandpiper (*Bartramia longicauda*)	4	32	0.1	0	32	0
Lesser Yellowlegs (*Tringa flavipes*)	1	11	0.1	0	11	0
Greater Yellowlegs (*T. melanoleuca*)	3	4	0.0	2	2	0
Whimbrel (*Numenius phaeopus*)	2	4	0.0	0	4	0
Least Sandpiper (*Calidris minutilla*)	3	4	0.0	0	4	0
Solitary Sandpiper (*T. solitaria*)	1	1	0.0	0	1	0
Red Knot (*C. canutus*)	1	1	0.0	1	0	0
Baird's Sandpiper (*C. bairdii*)	1	1	0.0	0	1	0
Common Snipe (*Gallinago gallinago*)	1	1	0.0	0	0	1
TOTAL	N = 30	21,252	100.0	11,501	5551	4200

[a] N values following season names indicate the number of censuses conducted during each season.

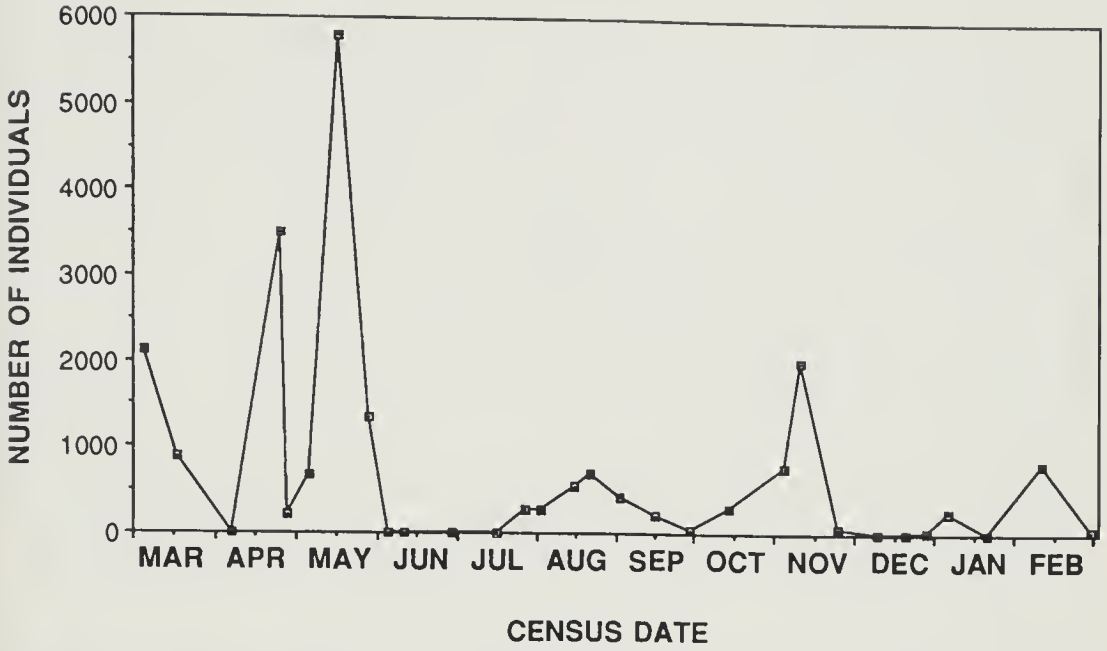

FIG. 2. Number of individual shorebirds foraging in agricultural fields during each census (Mar. 1991–Feb. 1992).

Plover, Upland Sandpiper, and Buff-breasted Sandpiper, fluctuated little during each of the four dawn-to-dusk surveys (Fig. 1). There were no significant differences in the abundance of these species in fields between high and low tides on 12 August ($t = 1.016$, df = 6, $P > 0.05$), 31 August ($t = 0.429$, df = 7, $P > 0.05$), and 2 November ($t = 1.000$, df = 6, $P > 0.05$). None of these species was observed during the 29 May survey.

Species composition and seasonal abundance patterns.—During the study of seasonal abundance patterns and cover use, I recorded a total of 21,254 individuals of 21 species of shorebirds foraging on croplands (Table 1). Shorebirds were observed foraging in agricultural fields on 24 of 30 censuses; no shorebirds were observed on two censuses in June and one each in April, July, January, and February. Only two individuals of one species (Willet) were observed during the four censuses in summer. Total shorebird species richness reached a peak of 18 species in fall, compared to 10 in spring and six in winter. This pattern also held for the mean number of species/census, being highest in fall ($\bar{x} = 8.4 \pm 6.9$ [SD]), intermediate in spring ($\bar{x} = 6.2 \pm 2.7$), and lowest in winter ($\bar{x} = 2.0 \pm 3.0$). In contrast, mean abundance/census was highest during spring ($\bar{x} = 2300.2 \pm 2320.8$ individuals/census) and lower in fall ($\bar{x} = 555.1 \pm 536.1$) and winter ($\bar{x} = 381.8 \pm 663.7$). ANOVAs confirmed that mean species richness/census ($F = 24.5$, $P < 0.001$) and mean shorebird abundance/census ($F = 4.83$, $P < 0.02$) did differ among seasons. In addition,

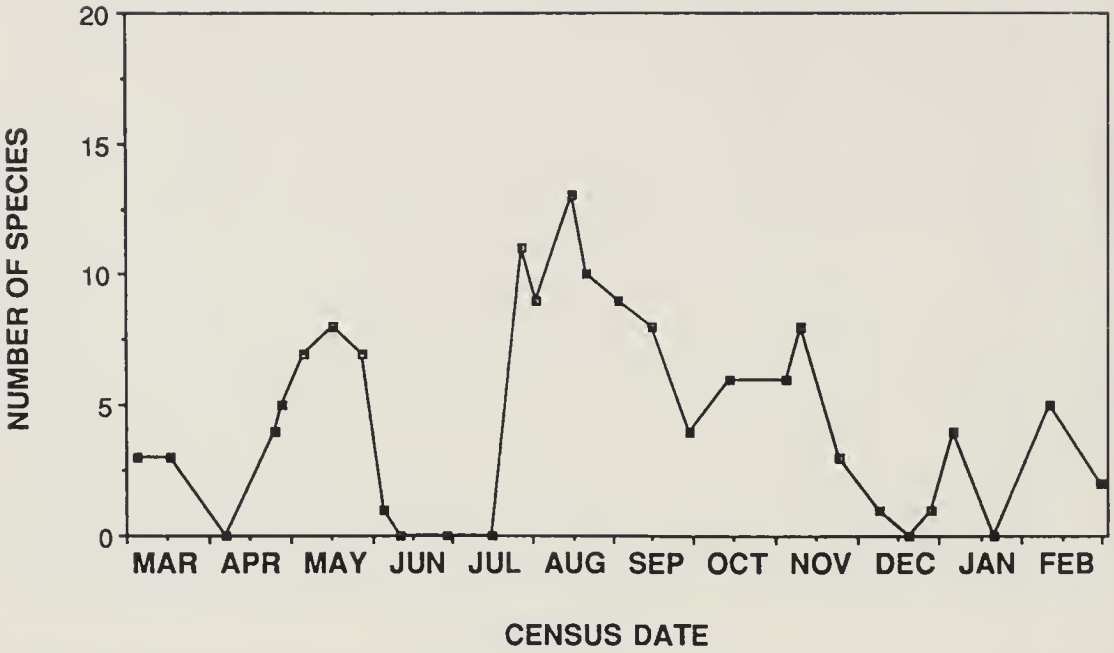

FIG. 3. Number of shorebird species foraging in agricultural fields during each census (Mar. 1991–Feb. 1992).

there was substantial variation in shorebird species richness and abundance within seasons as well.

The four species which were recorded on the most censuses (Black-bellied Plover, Killdeer, Semipalmated Plover, and Dunlin) were also the most abundant species, accounting for 94.3% of all the individuals observed. Most species were represented by relatively few individuals. Only 11 species were observed on more than four censuses, and only six species were represented by more than 90 individuals.

Whereas most species foraged in agricultural fields in only one or two seasons, Black-bellied Plover, Killdeer, Dunlin, and Short-billed Dowitcher were present during spring, fall, and winter. There were no species recorded year-round, as the only species present during summer (Willet) was not recorded in fall or winter. Of the remaining eight species represented by at least 30 individuals, four occurred strictly as fall transients (Pectoral Sandpiper, American Golden-Plover, Buff-breasted Sandpiper, and Upland Sandpiper), three were present only as spring and fall transients (Semipalmated Plover, Semipalmated Sandpiper, and Ruddy Turnstone), and one was present only during fall and winter (Western Sandpiper).

Because few of the fields were irrigated and rainfall was generally lower than average during the study period (U.S. Dept. of Commerce 1991), standing water was rarely present in the fields. As a result, species that require open water, such as Greater Yellowlegs, Lesser Yellowlegs,

and Solitary Sandpiper, were poorly represented on surveys. All other shorebirds usually foraged on relatively dry substrates, quite different from the saturated intertidal habitats with which the "field exploiter" species are more commonly associated.

Cover use.—A total of 19 species foraged on plowed fields, 17 species on fields with <10 cm cover, and seven species on fields with >10 cm cover. Although the number of species recorded on plowed fields was only slightly higher than the number on fields with <10 cm cover, far more individuals were observed foraging on plowed fields than on the other cover types. A total of 17,714 shorebirds, or 83.3% of all birds recorded during the study, foraged on plowed fields. In contrast, 3432 individuals (16.2% of total) foraged on fields with <10 cm vegetation and 108 birds (0.5% of total) on fields with >10 cm vegetation.

Of the species sufficiently numerous for analysis, all consistently showed highly significant positive assocations with plowed fields and negative assocations with fields with >10 cm cover except for Willet in spring and Upland Sandpiper in fall (Table 2). No species seemed actively to avoid plowed fields, and none was shown to prefer fields with >10 cm cover. The data for fields with <10 cm cover suggest that use of this cover type varied not only among species but also among seasons within a species. The proportion of species analyzed for cover use that showed positive associations with fields of <10 cm cover decreased from 0.71 in spring to 0.09 in fall and to 0.00 in winter. Conversely, the proportion of species negatively associated with fields of <10 cm cover increased from 0.14 in spring to 0.45 in fall and 1.00 in winter. For no species was the association with fields of <10 cm cover consistent among all seasons.

DISCUSSION

Agricultural fields on Virginia's Eastern Shore seem to be important foraging areas for migrating and overwintering shorebirds. A few species, such as Killdeer, American Golden-Plover, Upland Sandpiper, and Buff-breasted Sandpiper, are known to prefer such habitats to intertidal areas (Stout 1967, Hayman et al. 1986). These field specialists were never seen moving from fields to intertidal areas, and their numbers did not seem to vary with tidal height. Most of the species observed in this study, however, are known to prefer intertidal habitats when they are available. These field exploiters use fields as alternate foraging sites when mudflats and beaches are inundated by high water (Goss-Custard 1969, Page and Whitacre 1975, Gerstenberg 1979, Page et al. 1979).

Data from the four dawn-to-dusk surveys indicated that the abundance of field exploiters on cropland was high only within approximately two hours of high tide. Therefore, the surveys conducted to determine sea-

TABLE 2

COVER ASSOCIATIONS OF SHOREBIRDS FORAGING IN AGRICULTURAL FIELDS

Species	Total observed	No. observed/expected on each cover type[a]		
		Plowed	<10 cm	>10 cm
		Spring		
Black-bellied Plover	4664	3271/1323.1 ++	1383/ 415.7 ++	10/2925.2 −−
Semipalmated Plover	2822	2439/ 694.2 ++	233/ 209.4 ns	0/1918.4 −−
Willet	68	19/ 16.8 ns	27/ 7.9 ++	22/ 43.3 −
Ruddy Turnstone	51	38/ 10.0 ++	13/ 4.7 ++	0/ 36.3 −−
Semipalmated Sandpiper	502	483/ 108.7 ++	19/ 43.2 −−	0/ 350.1 −−
Dunlin	3252	2596/1150.3 ++	656/ 313.2 ++	0/1788.5 −−
Short-billed Dowitcher	138	108/ 45.1 ++	30/ 12.1 ++	0/ 80.8 −−
		Fall		
Black-bellied Plover	2033	1970/ 527.2 ++	61/ 388.6 −−	2/1117.2 −−
American Golden-Plover	57	50/ 8.7 ++	4/ 4.3 ns	3/ 44.0 −−
Semipalmated Plover	1299	1122/ 246.1 ++	132/ 97.4 +	45/ 955.2 −−
Killdeer	869	829/ 242.8 ++	38/ 177.7 −−	2/ 448.5 −−
Upland Sandpiper[b]	32	7/ 5.2 ns	4/ 2.5	21/ 24.3 ns
Semipalmated Sandpiper	58	58/ 8.3 ++	0/ 4.6 ns	0/ 37.2 −−
Western Sandpiper	34	33/ 9.1 ++	1/ 5.2 ns	0/ 19.6 −−
Pectoral Sandpiper	90	89/ 15.4 ++	0/ 5.9 −	1/ 68.7 −−
Dunlin	959	959/ 300.8 ++	0/ 262.6 −−	0/ 395.6 −−
Short-billed Dowitcher	53	53/ 16.1 ++	0/ 11.8 −	0/ 24.1 −−
Buff-breasted Sandpiper[b]	31	28/ 4.2 ++	3/ 2.0	0/ 24.8 −−
		Winter		
Black-bellied Plover	1285	1012/ 287.8 ++	273/ 755.5 −−	0/ 241.7 −−
Killdeer	169	145/ 28.8 ++	24/ 103.4 −−	0/ 36.8 −−
Dunlin	2700	2177/ 577.5 ++	523/1679.7 −−	0/ 442.8 −−
Short-billed Dowitcher	42	42/ 7.1 ++	0/ 22.4 −−	0/ 12.5 −−

[a] ns, $P > 0.05$; + and ++, significant positive associations ($P < 0.05$, $P < 0.001$ respectively), − and −−, significant negative associations ($P < 0.05$, $P < 0.001$ respectively).

[b] For these species, observed and expected numbers were pooled for plowed fields and fields with <10 cm to achieve expected values sufficiently high for testing.

sonal abundance and cover use patterns probably underestimated the use of croplands by field exploiters, as roughly half of the fields in each survey were visited 2–4 h preceding or following high tide. Because there was no apparent relationship between the times at which fields were visited and the cover types present in fields, this observation should have no effect on analyses of cover use.

Shorebird abundance in agricultural fields showed substantial variation among censuses. Fluctuations in abundance within (rather than among) seasons may have reflected differences in tidal height during the census periods. More shorebirds may have foraged in fields during higher peak

tides, when intertidal habitats were inundated for long periods, than during periods when high tide levels failed to inundate intertidal flats completely. In addition, variation in shorebird abundance within seasons may have been magnified by pulses of migration or regional movements that augmented or reduced shorebird abundance within the study area.

More individuals foraged in fields during spring migration than in any other season. This result may simply reflect larger numbers of birds passing through the study area in the shorter period of spring migration than during the more protracted fall migration. The compressed spring movement may also increase the shorebirds' need for rapid energy intake at staging areas (Pitelka 1979). If shorebirds benefit energetically from agricultural fields during high tide, then they should forage in fields during those periods when rapid energy intake is most critical (e.g., spring migration).

Agricultural fields were used by few species during winter, but of those present, most foraged in fields in high numbers. Because the threat of starvation to shorebirds may be quite high during winter (Goss-Custard 1979), alternate foraging areas such as coastal agricultural fields may enhance the chances of survival of overwintering shorebirds.

The type and structure of cover on which shorebirds forage may influence both predation risk and foraging efficiency. Despite the abundance of avian predators in the study area during winter, spring, and especially fall (pers. obs., Sutton 1992), most of the shorebird species in this study showed an overwhelming preference for plowed fields while avoiding dense vegetation.

Nearly all of the shorebirds observed were foraging in flocks, reducing the risk of depredation for any one individual during a predation attempt (Page and Whitacre 1975). Thus, flocking may have allowed the birds to forage relatively safely on plowed fields as they do on open mudflats and beaches. Flocking may also enhance foraging efficiency by allowing birds to share vigilance (Powell 1974, Metcalfe 1989). Sharing vigilance reduces the time that any one individual must spend looking for predators, thus increasing foraging time. Because vigilance sharing requires close contact among individuals and is inhibited in tall cover (Metcalfe 1984), vigilance sharing may not have been as profitable on vegetated fields as on plowed fields.

Foraging in plowed fields may also have been more efficient than on fields with >10 cm vegetation due to problems associated with foraging in dense vegetation. Because taller or more dense vegetation is thought to reduce the search area available to visual hunters, such as plovers (Fuller and Youngman 1979), or to inhibit locomotion and prey extraction, foraging on plowed fields may have been more efficient than on

fields with >10 cm vegetation. On fields with <10 cm cover, vegetation may not have been thick enough to impede efficient foraging in those species exhibiting positive associations with this cover type. Wind, extreme temperatures, and drought have been shown to reduce prey availability to a greater extent on bare earth than on vegetated cover (Burton 1974, Murton and Westwood 1974, Evans 1976, Shrubb 1988). However, given the year-round preference for plowed fields shown by most of the species in this study, these factors (and their seasonal variation) seem to have had little effect on the birds' preference for this cover type.

Although associations between most shorebird species and fields of bare earth or >10 cm vegetation were consistent among seasons, the use of fields with <10 cm cover showed substantial seasonal variation. Most significant associations with this cover type were positive in spring but negative in fall and winter. It is possible that the large numbers of shorebirds present in spring and the need to obtain energy rapidly during that season forced some shorebirds to forage on non-preferred cover types (e.g., <10 cm vegetation). Alternately, prey densities on these agricultural croplands may have been higher in spring than in other seasons, allowing efficient foraging on both plowed fields and fields with <10 cm cover during spring.

Because the periods of spring and fall migration require long-distance migrants to accumulate large energy reserves (Davidson 1984, Myers et al. 1987), and the threat of starvation to wintering shorebirds may be high (Goss-Custard 1979), coastal agricultural croplands may be important foraging areas for shorebirds during these periods. Where croplands are present near important shorebird staging areas, field management for foraging shorebirds may increase the value of the overall staging areas to these birds. Based on the results of this study, management regimes that provide an ample supply of plowed fields during periods of peak shorebird abundance might be most beneficial to shorebirds. Further research on the effects of field size, shape, or proximity to intertidal areas and of agricultural practices (e.g., plowing vs no-till farming, pesticide use, and timing of plowing and crop rotation) on shorebird abundance may facilitate the management of coastal agricultural lands for use by nonbreeding shorebirds.

ACKNOWLEDGMENTS

I am grateful to B. Watts, R. Beck, and M. Byrd for their help with study design and manuscript preparation. The manuscript also benefited from comments by C. Blem, A. Launer, J. Reaser, T. Wong, D. Shuford, and S. Melvin. I thank the Augusta and Monticello bird clubs and the College of William and Mary for their support of this study.

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Wilson Bull., 108(4), 1996, pp. 797–802

SHORT COMMUNICATIONS

Extra nest site occupancy by Tree Swallows: Do floaters avoid nest sites near settled pairs?—Tree Swallows (*Tachycineta bicolor*) are secondary hole-nesters for whom suitable cavities are a limiting resource (Holroyd 1975, Stutchbury and Robertson 1985). Despite nest site shortage, more than one cavity may be occupied by a single breeding pair (Rendell and Robertson 1994). Because Tree Swallows are single-brooded and generally monogamous (Robertson et al. 1992, but see Hussel 1983), the second site often goes unused. Occupancy of extra nest sites (ENSs) is therefore puzzling.

In this study we tested the hypothesis that ENS occupancy by Tree Swallows results from avoidance by floaters of nest sites near settled pairs. To date, most explanations of this behavior have assumed that a differential cost to defending the second site exists, and all have focused on benefits arising from its successful defense (Kendeigh 1941, Harris 1979, Robertson and Gibbs 1982, Muldal et al. 1985, Finch 1990, Dunn and Hannon 1991, Rendell and Robertson 1994). An alternative explanation is that floaters avoid or reject nest sites too close to already settled pairs. Residents may then occupy the extra sites without any increase in their total defense costs. That is, an ENS may be nothing more than a convenient perch from which to observe the primary site. The "avoidance hypothesis" sees ENS occupancy as an artifact of floater behavior rather than as resulting from the resident pair's defense and predicts that floaters will not make use of the nest sites in question even if the residents' defense radius is reduced. The hypothesis was noted in passing by Muldal et al. (1985) but has never been tested.

The avoidance hypothesis gains credibility from the observation that floaters in some Tree Swallow populations reject nest boxes placed in wooded areas or near forest edges (Harris 1979, Rendell and Robertson 1990, but see Erskine and McLaren 1976, Peterson and Gauthier 1985). The selectivity may reflect a risk at those nest boxes of egg destruction and nest site usurpation by House Wrens (*Troglodytes aedon,* Rendell and Robertson 1990) or a need for an open area nearby for foraging (Munro and Rounds 1985). If Tree Swallows are prepared to reject an otherwise suitable nest box because of its proximity to a forested area, might they also do so because of proximity to breeding conspecifics?

Floaters rejecting nest sites may lose breeding opportunities. Estimates of adult annual mortality in Tree Swallows range from 40–60% (Chapman 1955, Houston and Houston 1987) so delaying reproduction is risky. If Tree Swallows do avoid or reject nest sites near settled pairs, failure to do so must entail costs similar in magnitude to those of wren activity. This seems unlikely. Anecdotal accounts of Tree Swallows raising broods in nest boxes 1 m apart (Harris 1979) and even of two females laying in the same nest box (Quinney 1983, Muldal et al. 1985, Rendell 1992) suggest that floaters will breed near conspecifics rather than not breed at all.

To test the avoidance hypothesis, we arranged nest boxes in pairs and visually separated half those pairs with sheets of chipboard. Early in the season, breeding Tree Swallows defend their nest sites by spending the majority of their time perched at or near their nest holes (Leffelaar and Robertson 1984, Stutchbury and Robertson 1987a). Our visual barriers therefore made defense of a second box more difficult. Floaters locate unoccupied nest sites from the air and would be able to see both the unoccupied nest box and its proximity to an occupied box. If floaters avoid nest sites because of their proximity to already settled birds then barriers should have no effect. But, if defense of the extra nest box is important, then floaters should settle more often where barriers are present, i.e., we should observe two pairs of Tree Swallows breeding in adjacent nest boxes when barriers are present. As argued

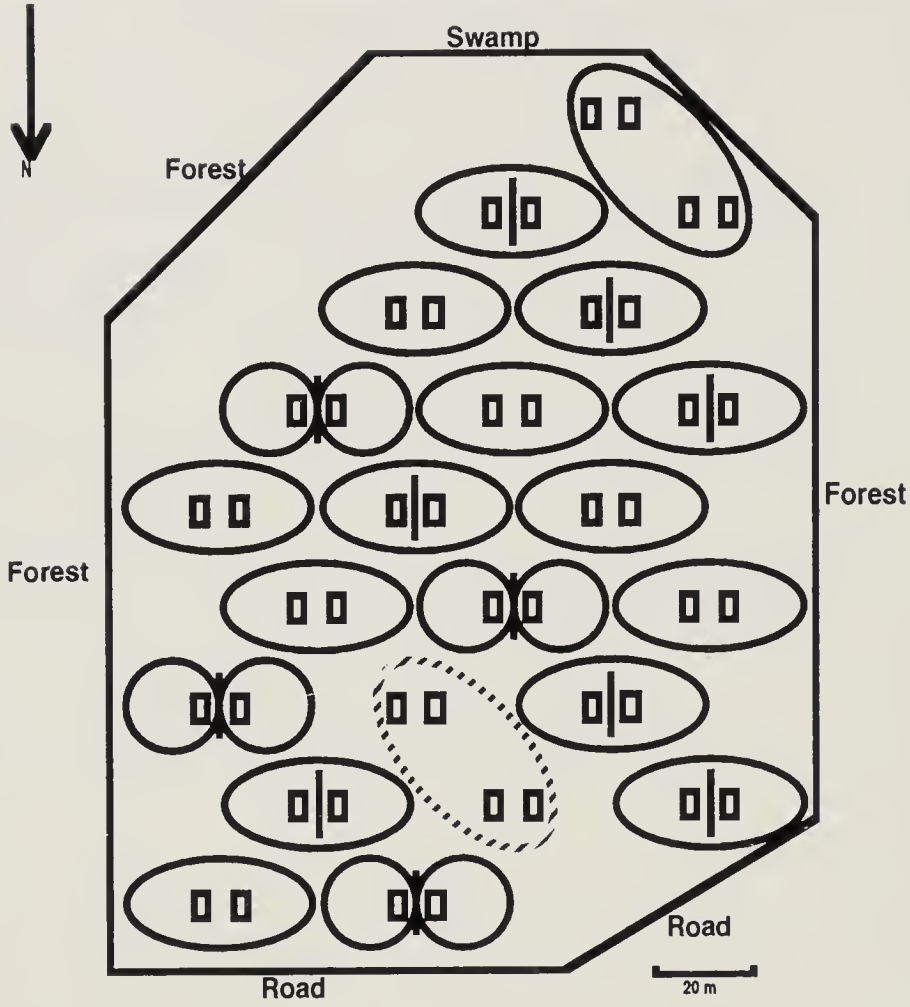

FIG. 1. Diagram of the Tree Swallow grid showing the arrangement of nest boxes (rectangles) and barriers (short vertical lines separating alternate nest box pairs) and the settlement pattern a day before the first egg was laid. Rings around cells or individual nest boxes indicate the nest boxes occupied by a pair of Tree Swallows and are not intended to delineate accurately the area defended. The dashed line ring around four nest boxes (two cells) circles the nest boxes occupied by a bigamous male; each female occupied one cell. Note that two control cells were occupied by one Tree Swallow pair (top right on the diagram) and that two pairs settled at each of four experimental cells.

above, we felt that the avoidance hypothesis, while plausible, was improbable and predicted that floaters would settle adjacent to a breeding pair more readily when a visual barrier was in place.

To avoid confusion between pairs of breeding Tree Swallows and paired nest boxes, we hereafter refer to the latter as cells.

Methods.—In late April 1991, we erected a grid of 44 nest boxes, arranged in 22 pairs (cells), on a 1.6 ha hayfield in Leed's County, Ontario (Fig. 1). Boxes were placed 1.5 m above the ground on aluminum poles. The two nest boxes of a cell were 8 m apart. Since Tree Swallows from this population normally defend a territory around a nest site of radius 15 m (Robertson and Gibbs 1982), we expected defense of a complete cell (two nest boxes) by each breeding pair. The shortest distance between nest boxes from different cells was 23

TABLE 1

NUMBER OF CONTROL AND EXPERIMENTAL PAIRED NEST BOXES (CELLS) AT WHICH BOTH NEST SITES WERE AND WERE NOT OCCUPIED BY A SINGLE BREEDING PAIR OF TREE SWALLOWS

	Barrier	No barrier
Extra nest site occupation maintained	7	11
Extra nest site occupation not maintained	4	0

m, which is greater than the normal defense radius, so defense of more than one cell by a breeding pair was not expected at either experimental or control cells.

At alternate cells down each row of the grid, we erected sheets of chipboard (1.2 × 2.4 m) between the nest boxes such that, from each nest box, the other, 8 m away, could not be seen. Chipboard sheets were visual barriers which, when present, made defense of both nest boxes in a cell more difficult for a breeding pair. Birds could not perch on the barrier because we put a tight line, strung with plastic drinking straws, about 1 cm above the top of each barrier. We refer to cells with chipboard obstructing the view of the adjacent box as barrier cells. The remaining 11 cells were control cells. Nothing obstructed the view of Tree Swallows perched on nest boxes at control cells.

Erecting barriers after settlement might have caused resident abandonment, so we put them up at the same time as the nest boxes, prior to Tree Swallow settlement. We could not detect any difference in any index of settlement date between control and barrier cells and, therefore, concluded that the presence of barriers did not affect the birds' nest box choice decisions (Mitchell 1992).

Residents were captured using mist nets and box traps (Cohen and Hayes 1984, Stutchbury and Robertson 1986) and marked with unique acrylic wing paint codes. Following banding, settlement and residency were determined using periodic 3–5 min watches at individual nest boxes and by regular examination of nest box contents.

Results.—Many Tree Swallow pairs initially occupied more than one cell. The number of breeding pairs then continued to increase throughout the breeding season until 28 active nests (eggs or nestlings present) were spread across the 22 cells and at least one breeding pair of Tree Swallows was present at every cell on the grid. We therefore had to pick a date on which to compare ENS occupancy frequencies at control and barrier cells. Costs and benefits of a second nest site may change following laying, so we decided to compare those frequencies on 13 May, a day prior to the laying of the first egg on the grid, at which time the grid held 25 active nests. Figure 1 shows the grid settlement pattern on 13 May. Occupancy of both nest boxes of a cell by a single breeding pair of Tree Swallows was significantly less common when a barrier separated the two boxes than at controls (one-way Fisher exact test, N = 22, m = 11,4, f = 0, $P = 0.04$) (Table 1). In fact, there were no cases where the two nest boxes of a cell were occupied by separate pairs of Tree Swallows except where a barrier separated those boxes.

The test is conservative since maintenance of two nest boxes broke down only at barrier cells; in addition, one Tree Swallow pair was still occupying two control cells (four boxes) and a bigamous male was also occupying two control cells, with each female occupying a single cell, at this time (Fig. 1). The bigamous two-cell occupation remained stable for the duration of the breeding season. The two-cell occupation ended when the original female started laying at one cell, whereupon a new Tree Swallow pair settled at the second cell.

This was the twenty-sixth active nest. No Tree Swallow was occupying more than one barrier cell at that time.

Approximately four weeks after the initial settling, females settled at the unused nest boxes at one barrier and one control cell following the hatching of the original females' clutches. These may have been lone females or may have been paired with the original resident male. Only the new females fed the nestlings.

We observed several resident females, at both barrier and control cells, adding nesting material to both nest boxes of cells involved in ENS occupancy. In each instance, though, eggs were laid in only one of the boxes. Where pairs occupied extra nest sites, both residents spent time at each nest box and both responded aggressively to intruders, although it was not possible to determine to which box a threat was perceived.

Discussion.—The lower frequency of ENS occupancy when adjacent nest boxes were separated by a visual barrier permits rejection of the avoidance hypothesis. When the ability of a resident to defend a second nest box was experimentally reduced, floaters settled and bred in boxes 8 m from existing pairs. Floaters may prefer to nest at greater distances from conspecifics, but this preference is not a sufficient explanation for ENS occupancy. It is fair to characterize ENS occupancy as ENS defense.

We emphasize that our result cannot simply be an outcome of barriers causing settling floaters to be unaware of their neighbors or residents to be unaware of a nearby nest box. While territory defense is accomplished through time spent perched at a nest site, floaters searching for nest sites do so by flying through a colony repeatedly (Stutchbury and Robertson 1987b) and thus should be aware of a neighbor's presence. The ability of seven Tree Swallow pairs to maintain two nest boxes despite the presence of a barrier demonstrates that the second box's presence is recognized by the resident pair and that defense is possible.

Rendell and Robertson (1994) found that male Tree Swallows, and possibly females, preferred territories on which a second nest box could easily be defended (because of the proximity of adjacent nest boxes). Mitchell (1992) detected no evidence of preference for control cells by Tree Swallows in his study, but the rapid pace of settlement and our small sample size could have masked such a preference. If a preference did exist, it was not sufficient to induce settling Tree Swallow pairs to reject cells consistently where barriers were present. Therefore, our conclusion remains unchanged: Avoidance by floaters is an insufficient explanation for ENS occupancy by Tree Swallows.

Using model intruders, Robertson and Gibbs (1982) concluded that Tree Swallows defend a circular territory around a primary nest box and occupy additional nest boxes which happen to lie within that radius. That hypothesis has since been refuted by Rendell and Robertson (1994) who found that Tree Swallows occupied nest sites up to 56 m apart. These findings raise a question that has thus far not been addressed: When a resident Tree Swallow is observed responding aggressively to an intruder, how can one determine whether the resident perceives a threat to its primary nest site or to an ENS? Our study succeeds in rejecting the avoidance hypothesis without using observations of aggressive behavior. However, we suspect that distinguishing between two remaining hypotheses will require such observations.

Rendell and Robertson (1994) argued that ENS defense by pairs of Tree Swallows results from an intersexual conflict of interest. Males defend an ENS in hopes of becoming polygynous. Females then defend the same extra site to ensure male monogamy. Rendell and Robertson (1994) could not convincingly reject an alternative hypothesis that Tree Swallow pairs cooperate in defense of an ENS as a site for renesting should their first attempt fail. These hypotheses reflect fundamentally different views of territorial behavior. Not only does the explanation for ENS defense differ, but the perceived relationship between members of the breeding pair differs.

If aggressive behavior can be unequivocally assigned to defense of an ENS, then the two explanations can be distinguished by looking at which sex male and female Tree Swallows defend a second site against. If a polygyny-monogamy conflict is involved, females should respond aggressively to intruding females but ignore or actively encourage intruding males, since settlement by a second male removes the risk of polygyny for the female. Male Tree Swallows' pattern of aggression should be just the opposite. If defense is cooperative, both male and female Tree Swallows should defend an ENS against intruders of either sex.

This distinction was not possible in our study, in which paired nest boxes were only 8 m apart. However, the comparison would be worthwhile when the two nest sites are more widely separated, as in some of the cases reported by Rendell and Robertson (1994) and where floaters have been captured, sexed, and individually marked.

Acknowledgments.—Stan Teeple generously allowed us to use one of his hayfields as a study site. Beth MacDougall, Melanie Sharman, Lisa Venier, and Linda Webster assisted with grid construction, and Grace Erb with banding and observations. Andrew Chek, Floyd Connor, Kelvin Conrad, Peter Dunn, Frank Phelan, Susan Meek, Laurene Ratcliffe, and Linda Whittingham provided useful criticism of the design and interpretation of this study. The Queen's Univ. Biological Station provided logistic support. The study was funded by NSERC and SEED grants to RJR. JSM was supported during preparation of the manuscript by an NSERC Postgraduate Scholarship.

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Wilson Bull., 108(4), 1996, pp. 802–804

Swainson's Warblers nesting in early seral pine forests in East Texas.—Swainson's Warbler (*Limnothlypis swainsonii*) breeds locally throughout the southeastern United States on the south Atlantic and Gulf coastal plains, in the southern Appalachians, and on the southern Piedmont Plateau (Meanley 1966). They select areas with low, dense understories (Eddleman et al. 1980, Meanley 1971). Meanley (1945, 1966, 1969) described several habitats of Swainson's Warblers in the eastern coastal plains, and they also have nested in dense rhodendron-laurel thickets in the southern Appalachians (Brooks and Legg 1942). However, there is little information on the specific habitat features which may influence the distribution and abundance of this species, especially in the western portion of its breeding range. In this paper, I report on the first described use of early seral pine forests by Swainson's Warblers nesting in eastern Texas. I compare habitats selected in this study to those previously described and suggest possible relationships between habitat selection and abundance patterns.

I surveyed for Swainson's Warblers from April through June 1992 on the San Jacinto Ranger District, Sam Houston National Forest, San Jacinto County, Texas (95°07′W, 30°30′N). The district consists of approximately 24,000 ha of pine, pine-hardwood, and bottomland hardwood forest of various age classes. The district is managed for timber production, recreation, wildlife, and some oil and mineral extraction. Timber is managed primarily in even-age stands ranging from 4–40 ha on 70-year rotations. Harvest methods include thinning, clearcuts, seed-tree cuts, and shelterwood cuts. Large areas regularly are

prescribed burned. I used playback recordings to detect territorial males, primarily along maintained roads, old logging roads, and trails which transect much of the district. Males captured in mist nets were banded with unique combinations of colored leg bands and a U.S. Fish and Wildlife Service aluminum leg band. I located territories and determined whether each male was paired. I considered an individual interacting with another bird within the territory without hostile behavior to be paired. I returned to each territory 2–4 times during the breeding season. Stand ages were determined using the Continuous Inventory of Stand Condition database maintained by the U.S.D.A. Forest Service.

I monitored 38 territories during the 1992 season. Eleven (28.9%) territories were in loblolly pine (*Pinus taeda*) plantations (age range = 3–18 yrs; mean age = 14.0 ± 4.2 yrs) with dense understories composed primarily of yaupon (*Ilex vomitoria*), *Smilax* spp., *Viburnum* spp., and various sapling hardwood species. Sixteen (42.1%) were in sites previously logged to remove pine, infested with southern pine beetles (*Dendroctonus frontalis*). These sites ranged from 1–2 ha in size and were dominated by a dense growth of early successional shrub species and sapling trees. The remaining 11 (28.9%) territories were in relatively mature stands of loblolly pine with a sparse overstory and patches of dense understory. Eight of these territories were in mesic sites near streams or ephemeral forest swamps. The remaining three were in relatively xeric upland stands with a mixed pine-hardwood overstory and dense yaupon understory.

I confirmed nine paired males: three in plantations, five in logged sites, and one in a mature stand. I found a probable Swainson's Warbler nest in an active territory in a pine plantation on 21 May 1992. The nest closely resembled photographs by Graves (1992) and possessed the bulky outer layer of dead hardwood leaves characteristic of the species (Meanley 1969). The nest was empty and appeared to have been abandoned or predated since no eggs or young were observed during six visits I made the following three weeks. I observed an adult Swainson's Warbler foraging approximately 2 m from the nest during the first visit. The nest was approximately 1 m high and supported by a tangle of *Smilax* spp. suspended in pine saplings. I observed one pair feeding fledged young in a logged site located within the territory of the male. The young were still incapable of sustained flight and were more than 20 m within the logged site.

Early seral pine forest previously has not been described as potential breeding habitat for Swainson's Warblers. They generally use areas with a low, dense deciduous understory (Meanley 1971). River floodplain forest with dense understories of cane (*Arundinaria gigantea*), sweet pepperbush (*Clethra alnifolia*), or scrub palmetto (*Sabal minor*) have been identified as important breeding habitats on the upper and Gulf coastal plains (Meanley 1971). Swainson's Warblers in the southern Appalachian Mountains use dense rhodendron-laurel thickets in mature hardwood communities (Brooks and Legg 1942). Eddleman et al. (1980) found several territories in areas dominated by early successional tree species, such as sweetgum (*Liquidambar styraciflua*) plantations, and in late old field habitats with dense shrubs. These habitats possess a dense understory structure comparable to the pine plantations and logged sites used by Swainson's Warblers in eastern Texas. The understory foliage diversity patterns of these different habitats would probably be relatively similar despite differences in plant species composition, suggesting vegetative structural patterns may be an important factor influencing habitat selection and distribution of Swainson's Warblers.

Man-made areas of early seral forest, such as pine plantations and logged sites, may represent new habitat options for breeding Swainson' Warblers. There is no evidence to suggest that such habitat resulting from normal forest succession was not used in addition to historically abundant canebrake habitat. Cane was formerly a dominant understory feature of the lowlands of eastern and southeastern Texas, but with the introduction of domestic livestock, it has become relatively rare (Correll and Johnston 1970). Swainson's Warblers

appear common on the San Jacinto Ranger District, despite the lack of cane habitat. The paired individuals and nesting activity observed in pine plantations and logged sites suggests such areas may be important breeding habitat.

Apparent flexibility of habitat use by Swainson's Warblers may explain its relatively stable population in contrast to the decline of the Bachman's Warbler (*Vermivora bachmani*). The Bachman's Warbler may have been a cane specialist, and the probable extinction of the species parallels the decline of cane stands throughout the southeastern United States (Widmann 1897, Remsen 1986). The more generalist strategy of the Swainson's Warbler may have enabled it to continue exploiting alternative habitats such as dense thickets in forest openings to maintain population levels.

Acknowledgments.—I thank the staff of the San Jacinto Ranger District, Sam Houston National Forest, for assistance during this project. L. J. Carmical provided access to the district and Forest Service records. Comments from R. E. Brown, D. K. Carrie, R. N. Conner, J. Nelson, and D. C. Rudolph improved an earlier draft of this manuscript.

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Wilson Bull., 108(4), 1996, pp. 804–807

Measurements of Snail Kite eggs from central Florida.—The Snail Kite (*Rostrhamus sociabilis*) is a raptor with a disjunct distribution among several lake and everglade wetlands in central and south Florida (Sykes et al. 1995). The objectives of the present study were to collect measurements of kite eggs, delimit egg size variation among wetlands, and determine if egg size was correlated with clutch size, hatching success, fledging success, and breeding chronology of kites in central Florida.

Methods.—I visited Snail Kite nests every 1–2 weeks during 1991 at East Lake Toho-

TABLE 1
LINEAR MEASUREMENTS AND CALCULATED VOLUMES OF SNAIL KITE EGGS FROM CENTRAL FLORIDA[a]

Site	Variable	N	$\bar{x} \pm$ SD	Range
East Lake Tohopekaliga	Length	15	44.27 ± 1.16 mm	41.9–47.2 mm
	Breadth	15	36.56 ± 0.74 mm	35.1–37.8 mm
	Volume	15	30.20 ± 1.58 cm^3	26.33–32.37 cm^3
Lake Tohopekaliga	Length	254	44.33 ± 1.74 mm	40.0–48.4 mm
	Breadth	254	36.38 ± 0.90 mm	32.3–38.5 mm
	Volume	254	29.97 ± 2.27 cm^3	22.67–34.77 cm^3
St. Johns Marsh	Length	57	44.46 ± 1.53 mm	40.2–47.5 mm
	Breadth	57	36.41 ± 1.22 mm	33.6–40.1 mm
	Volume	57	30.14 ± 2.87 cm^3	24.07–37.64 cm^3
Lake Kissimmee	Length	129	43.90 ± 1.64 mm	40.5–49.1 mm
	Breadth	129	35.91 ± 1.11 mm	33.2–38.5 mm
	Volume	129	28.94 ± 2.61 cm^3	22.77–35.61 cm^3
Lake Okeechobee	Length	250	44.21 ± 1.35 mm	41.0–48.6 mm
	Breadth	250	36.21 ± 0.98 mm	33.7–39.4 mm
	Volume	250	29.61 ± 2.21 cm^3	24.67–38.28 cm^3
Total	Length	705	44.22 ± 1.57 mm	40.0–49.1 mm
	Breadth	705	36.24 ± 1.01 mm	32.3–40.1 mm
	Volume	705	29.67 ± 2.38 cm^3	22.67–38.28 cm^3

[a] Egg volume = 0.51 × length × $breadth^2$.

pekaliga, Lake Tohopekaliga, Lake Kissimmee, Lake Okeechobee, and an impounded marsh at the headwaters of the St. Johns River (hereafter St. Johns Marsh). Eggs were numbered with an indelible felt-tip pen according to deposition sequence when known. Length and breadth measurements were made with a Tajima dial caliper (model dial-15) to the nearest 0.1 mm. Egg volume was estimated using the equation of Hoyt (1979): volume = 0.51 × length × $breadth^2$. Relative egg volume used in some statistical analyses was calculated after Arnold (1991): individual egg volume minus the mean egg volume of the clutch divided by the standard deviation of egg volume for the clutch.

All computations were preformed using SAS Institute, Inc. software. Length, breadth, and volume were found to be normally distributed (Shapiro-Wilk test, $P > 0.05$; SAS Institute 1990). A plot of the residuals versus the predicted values from an ANOVA model using PROC GLM (SAS Institute 1990) yielded a random scatter that suggested homogencity of variance for the three variables. Thus, parametric statistics were used in all subsequent analyses. Mensural variables were determined for both complete and incomplete clutches. However, only data from complete clutches were used when comparing egg size with clutch size, hatching order, hatching success, and fledging success. Logistic regression in PROC GENMOD (SAS Institute 1996) was used to analyze hatching and fledging success since these data are binomial. Hatch date was a convenient index for breeding chronology and was determined as the week of hatching for the first egg in each clutch.

Results.—I calculated mean, standard deviation, and range of length, breadth, and volume of 705 eggs from 260 complete and incomplete clutches of Snail Kites (Table 1). The relation

of mensural variables was length = 0.81 breadth (Pearson's $r^2_{704} = 0.52$, $P < 0.0001$). No significant difference (ANOVA, $F = 1.97$, df = 704, $P = 0.10$) was detected in length among the five wetlands. However, significant differences were found in breadth (ANOVA/Fisher's LSD test, $F = 5.58$, df = 704, $P = 0.0002$) and volume (ANOVA/Fisher's LSD test, $F = 4.87$, df = 704, $P = 0.0007$). Eggs from Lakes Kissimmee and Okeechobee consistently exhibited the smallest mean breadth and volume (Table 1).

No significant difference was found in length (ANOVA, $F = 1.70$, df = 46, $P = 0.19$), breadth (ANOVA, $F = 0.15$, df = 46, $P = 0.86$), or relative volume (ANOVA, $F = 0.60$, df = 46, $P = 0.55$) among the first, second, or third egg hatched. There also was no significant difference (ANOVA, $F = 1.41$, df = 238, $P = 0.24$) in mean relative egg volume among clutches of one (N = 3), two (N = 52), three (N = 169), and four (N = 8) eggs. Thus, egg size was similar regardless of laying order or clutch size.

Relative volume was not correlated with hatch date at East Lake Tohopekaliga ($r^2_{13} = 0.05$, $F = 0.63$, $P = 0.44$), Lake Tohopekaliga ($r^2_{252} = 0.002$, $F = 0.60$, $P = 0.44$), Lake Okeechobee ($r^2_{248} = 0.006$, $F = 1.52$, $P = 0.22$), and St. Johns Marsh ($r^2_{55} = 0.001$, $F = 0.04$, $P = 0.84$), except at Lake Kissimmee ($r^2_{127} = 0.059$, $F = 5.18$, $P = 0.02$). Thus, volume generally did not exhibit intraseasonal variation at most wetlands. Finally, relative volume was not correlated with hatching success ($P = 0.88$, df = 155) or fledging success ($P = 0.99$, df = 227) of kite nestlings.

Discussion.—The mensural values of my study are similar to the average length (44.6 mm, N = 317 eggs) and breadth (36.1 mm) reported by Sykes (1987). Although Snail Kite eggs exhibited differences in breadth and volume among my study sites, I found little correlation with clutch size, laying sequence, and hatching date. Kites are similar to other avian species whose egg sizes do not correlate with laying sequence (Pulliainen and Saari 1993), clutch size (Ojanen et al. 1981, Jover et al. 1993), or laying date (Arnold 1991, Potti 1993, Pulliainen and Saari 1993).

An increase in egg size during the laying sequence has been suggested as a strategy by females to adjust their egg contribution to the initial nestling size disadvantage due to asynchronous hatching (reviewed by Magrath 1992). However, size and volume of Snail Kite eggs were not correlated with laying sequence and fledging success. Kites neither support the brood reduction strategy (reviewed by Magrath 1992) that egg size decreases with laying order nor the bet-hedging strategy (reviewed by Slagsvold et al. 1984) that egg size increases with laying order. Because egg volumes within a clutch and among different clutch sizes were similar, the competitive ability of Snail Kite nestlings results mainly from hatching asynchrony and the ability of parents to secure adequate snails to feed their young. Magrath (1992) suggested hatching asynchrony was more important than egg mass in determining hatch size hierarchies and resultant early nestling survivorship. Significant differences in egg breadth and volumes among wetlands suggest local effects on egg sizes but not the fledging success of Snail Kites during the single breeding season of my study. These differences warrant further study to establish if a relationship exists between habitat quality and condition of females with nestling survival during more stressful years.

Acknowledgments.—Funding for this study was provided by Section 6 funding from the U.S. Fish and Wildlife Service and the Nongame Wildlife Program of the Florida Game and Fresh Water Fish Commission. S. T. Schwikert assisted me with the data collection. S. B. Linda provided statistical consultation. I thank M. F. Delany, S. A. Nesbitt, D. A. Wood, P. W. Sykes, C. R. Blem, and an anonymous referee for reviewing an earlier draft of the manuscript. This research was part of study number 7520 of the Bureau of Wildlife Research.

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Wilson Bull., 108(4), 1996, pp. 807–808

The Andean Flamingo in Brazil.—Bege and Pauli (1990a, b) recorded the Andean Flamingo (*Phoenicoparrus andinus*) for the first time in Brazil, based on an emaciated juvenile found in May 19, 1989 in Erval Velho (27°13′S, 51°23′W), midwest of Santa Catarina State that had been banded in Chile. The specimen is now housed in the Museu Nacional, Rio de Janeiro (MN 36.548). Antas (1990) also recorded a subadult bird foraging at the Lagoa do Peixe (31°20′S, 51°05′W), southeastern Rio Grande do Sul, along with the Chilean Flamingo (*Phoenicopterus chilensis*).

The Museu do Seminário Coração de Jesus, in Corupá, Santa Catarina, houses a juvenile specimen (MSCJ 220) obtained in 1952 at Jaraguá do Sul (26°28′S, 49°06′W), northeastern Santa Catarina, which was wrongly identified by Sick et al. (1981) as an American Flamingo (*Phoenicopterus ruber*). This specimen is a well preserved, mounted skin. To Rio Grande do Sul we have an additional record based upon a color photograph of three adult birds in Lagoa do Peixe, taken in the fall of 1992 (A. Hoffmann, pers. comm.). It was published

without proper identification by Porto (1992). At the time, many flocks of Flamingos were recorded and photographed by Hoffmann.

Silva and Caye (1992) reported the Andean Flamingo as accidental in Rio Grande do Sul and Bornschein (1992) also considered as such the occurrence of this species in Brazil. However, it is quite likely that the Andean Flamingo migrates to Rio Grande do Sul with more frequency than previously supposed, given the current number of records (fide Hoyo et al. 1992, La Peña 1992). It is worth thus to stress the care in identifying Flamingos in southern Brazil, where *Phoenicopterus chilensis* is a regular species, mainly in the winter (Belton 1994).

Acknowledgments.—We thank Jorge B. Nacinovic. Jorge Baldo, Alejandro R. Giraudo, and Dante M. Teixeira for confirmation identification of the flamingo in a photograph published in the magazine *Globo Rural,* and J. B. Nacinovic also for text revision and translation. J. Baldo also sent us a color photograph with the details of the bills of *Phoenicoparrus andinus, P. jamesi* and *Phoenicopterus chilensis,* which helped us identify the specimen in the museum in Santa Catarina.

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Marcos R. Bornschein and Bianca L. Reinert, *Museu de História Natural "Capão da Imbuia", Rua Prof. Benedito Conceição 407, Curitiba (PR), Brazil, 82810-080.* *Received 9 Oct. 1995, accepted 21 March 1996.*

Wilson Bull., 108(4), 1996, pp. 809–812

ORNITHOLOGICAL LITERATURE

Edited by William E Davis, Jr.

Avian biochemistry and molecular biology. By Lewis Stevens. Cambridge University Press, Cambridge, U.K. 1996:272 pp. $50.00 (cloth).—A synopsis on the first page of this book says it is ". . . the only comprehensive and up-to-date survey of avian biochemistry and molecular biology available." The author has written a clear and concise coverage of this area. The text covers such aspects as protein and amino acid metabolism, nutrition, lipids, carbohydrates, avian hormones, and metabolic adaptation. Part 2 of the book is devoted to "the avian genome and its expression" and summarizes this material not available elsewhere.

The text is nicely organized and cleanly presented. The figures are nicely done and relevent to the account. There were few, if any, typographical errors. The references are fairly thorough and up-to-date, although I suspect United States authors are a bit underrepresented in the review. I was impressed that the author appreciated correct nomenclature and taxonomy and made an effort to use it in a book that essentially is about molecular biology. It frustrates me to see manuscripts about birds written by people who are not sufficiently informed to recognize appropriate nomenclature.

This text is well worth the money for those interested in the cellular-molecular level of ornithology.—C. R. Blem.

Orioles, blackbirds, and their kin: a natural history. By Alexander F. Skutch. Illus. by Dana Gardner. The University of Arizona Press, Tucson, Arizona. 1996:291 pp. $50.00 (cloth), $21.95 (paper).—Who says there are no more heroes to emulate? Mine easily could be Alexander F. Skutch. At time when study of whole organisms is considered passé by some, Dr. Skutch has produced a masterful account of the natural history of a very important group—the blackbirds (and after his 90th birthday!). This book, his twenty-sixth, guides us to through a detailed, but never boring, account of how the orioles, blackbirds, and their kin go through their lives. Some accounts were taken, "with slight modifications" from Skutch's *Life histories of Central American birds*, published in 1954 by The Cooper Ornithological Society, and from a few other miscellaneous published sources. The material has been updated with references cited from the scientific literature through 1994, and new accounts were added.

Skutch writes clearly, cleanly, and with a lot of content. To my taste he adds just enough anthropomorphism to be interesting, but not unscientific. The book includes historical vignettes, personal asides, and insightful comments—all done in an economical, interesting manner. The sections on cowbirds alone are worth the price of the book. Beginning birders will enjoy the book and learn a great deal of fundamental ornithology. Advanced students will find much useful information and introduction to specific references. The reference section is not (nor was it intended to be) a comprehensive coverage of the blackbirds and their kin.

Gardner's black-and-white sketches are excellent, the binding and covers attractive, and the book is well worth the money (particularly the paperback version). All-in-all this is a wonderful book. It stands as an example of the way in which bird books of this genre should be done.—C. R. Blem.

FINDING BIRDS IN SOUTHEAST ARIZONA. By the Tucson Audubon Society Publications Committee. Tucson Audubon Society, Tucson, Arizona. 1995:347 pp., color photographs, maps, bar-graphs. $16.95 (wire-O binding).

A BIRDER'S GUIDE TO SOUTHEASTERN ARIZONA. By Richard Cachor Taylor. American Birding Association, Inc., Colorado Springs, Colorado. 1995:x + 342 pp., black & white photographs, drawings, maps, bar-graphs. $16.95 (wire-O binding). Here we have the two newest bird finding guides to some of the hottest hot spots in North America—the canyons, deserts, and oases of southeastern Arizona. I am writing this review from the point of view of a New Englander who has visited southeastern Arizona three times chasing birds, mammals, herptiles, and butterflies. When I next go back, should I take along both of these books or will one suffice?

Physically, the books are nearly identical—same height, width, and thickness and same "wire-O" spiral binding with wrap-around back cover. By the way, who ever thought up these wrap-around covers? They are awful. If they did not have maps printed inside them, I would cut off the wrap-around flaps in an instant.

Every good bird finding guide should give the reader help in deciding when to visit, what to wear, and where to stay. Both of these guides offer sound advice on these subjects. Books of this genre should also provide a general introduction to biomes and climate, and in this regard the Audubon Society book is superior, providing color photographs of typical habitats. The Audubon Society guide also offers nine pages of timely advice to the would-be visitor to Mexico and this is a definite plus.

The main body of text in these guides is in two or three parts and includes maps of, directions to, and discussions of the best birding locales; seasonal bar-graphs; and comments on selected species. First, the birding areas: As a three-peater, I have my favorite spots in southeastern Arizona, so I chose four—Madera Canyon, the Chiracahua Mountains, Mount Lemmon, and the Patagonia-Sonoita Creek Preserve—to compare coverage between the two books. "Finding Birds in Southeastern Arizona" covers these four areas with 26 pages of text and six maps; "A Birder's Guide to Southeastern Arizona" uses 57 pages and nine maps. Everything about the ABA guide is superior in this crucial section of the text. The maps are clearer, and nothing is more important than a clear map! Taylor's text offers keener insights into all that is new and wonderful along the way, and although there is an unnecessarily greater emphasis placed on rarities, his are the words I would choose to follow. Not only are there a lot more pages of description of these sights, there are considerably more words per page in the ABA guide and so the reader has more than 2.5 times the text in Taylor's book, at least on these sites.

Second, the seasonal bar-graphs: In a word, they are excellent in both books. To the serious bird student, these bar-graphs are gold mines. I must admit I favor simple, straightforward bar-graphs and for this reason I prefer those in the Audubon Society guide; too much "going on" in the ABA bar-graphs.

Third, discussions of selected species: The ABA guides always contain an enlightening chapter on "Specialties," those species that for one reason or another birders most want to see. *A Birder's Guide to Southeastern Arizona* offers up a long list of specialties, along with information on locating and identifying them. *Finding Birds in Southeastern Arizona* includes annotations on *all* of the birds of the region, not just the "most wanted," and this is noteworthy and commendable.

Now, back to the original question. Do I buy both books and pack them along to Arizona or do I choose between the two? Personally, I like to have as many compact nature guides along as I can fit in a small box in the middle of the front seat of my rental car. I would get them both, since each has outstanding features lacking in the other. However, if I ab-

solutely had to choose, Richard Taylor's "A Birder's Guide to Southeastern Arizona" would have pride of place in my luggage.—Brian E. Cassie.

Barn Owls: predator–prey relationships and conservation. By Iain Taylor. Cambridge University Press, Cambridge. 1994:xvi + 304 pp., 46 photographs, 28 drawings, 81 graphs and tables, 2 maps, 2 appendices. $37.95 (cloth).—The Barn Owl (*Tyto alba*) ranges across the warmer regions of six continents and perhaps has been as well studied as any owl species in the world. The author of the present study has chosen to present the ecology, biology, and conservation of the Barn Owl primarily through an investigation of the relationships between this bird and its prey. Taylor's study area was in southern Scotland and with the help of co-workers and local farmers, he managed to keep track of all of the Barn Owls in his 1600 km^2 main study site, as well as those in two smaller replicate study areas. His studies, conducted from 1978–1992, as well as field research studies from other parts of the world, especially in New Jersey and Utah, form the basis of this book.

After a short introduction to the Barn Owl and the author's research area and methods, the book presents chapters on distribution, diet, foraging behavior, ecology and behavior of the prey, prey selection and foraging habitats, ranging and roosting behavior, molt, breeding seasons, nest sites, courtship and eggs, production of young, dispersal, mortality, population size and regulation, and conservation. Two conventions that will make using this book particularly easy for researchers are the use of headings on the right-hand pages and the inclusion of a summary as each chapter's conclusion. If only all authors and editors took the time to include these! There is a 365-reference bibliography and the illustrations and graphs are well done.

Of course, not everyone who picks up Iain Taylor's book is or will be an owl biologist. Most, I assume, will be interested in owls in general and will want to know if the biology and ecology presented are sound and if the book is readable. They will want to read the book, not merely "use" it. For all of them (and you), owl fanciers and research biologists alike, the book is very highly recommended. Taylor's discussions are first-rate: well researched, well written, and thought provoking. When there are suspect references in the literature, Taylor questions them. When research is lacking into some aspect of the Barn Owl's life, Taylor points this out and offers suggestions to future researchers. This book is an outstanding model for comprehensive, well structured, and enjoyable scientific literature.—Brian Cassie.

The Megapodes *Megapodiidae*. By Darryl N. Jones, René W. R. J. Dekker, and Cees S. Roselaar, illus. by Ber van Perlo. Oxford University Press, New York. 1995:262 pp., 8 color plates, 24 range maps, 18 numbered text figs., 5 tables. $60 (cloth).—This family of galliform-like birds is unique in that all members use some form of naturally occurring heat to incubate their eggs, earning them the vernacular names of "thermometer" or "incubator" birds. Some species build mounds and use heat from the decomposition of damp organic matter, while others use burrows and geothermal heat or solar-heated volcanic sand. The chicks are extremely precocious, digging their way out of incubation mounds or burrows without assistance, capable of flight on the day of hatching, and receiving no subsequent parental assistance.

This third volume in Oxford University Press' series on bird families of the world provides a thorough treatment of this fascinating family which is restricted to the Indo-Australia and

Pacific Islands area. The monograph is divided into two parts, the first nine chapters deal with aspects of the biology and conservation of megapodes; the second part includes accounts of the seven genera and 22 species. Chapter two deals with the rather problematical taxonomy of the group. Here megapodes are treated as the sister group of all other galliformes instead of a sister group of cracids. The authors also conclude that brush-turkey genus *Talegalla* is not as closely related to *Alectura* and *Aepypodius* as had previously been considered and this is used as justification for changing the common name of the three *Talegalla* species from brush-turkey to talegalla. They describe three new subspecies in the genus *Megapodius* in which they include 13 species (the number recognized in various taxonomic schemes over the years has varied from three to 19). They also changed the name of *Megapodus* species from scrubfowl to megapode. I consider both of these name changes ill-advised. I object to using genus names as common names because, unless you are a Greek and Latin scholar, they are not as descriptive as English names ought to be. The use of megapode for a subset of the megapodes (the title of the monograph) provides lots of room for confusion.

The third chapter deals with megapode distribution, biogeography, and speciation, and the fourth discusses behavior and demonstrates the link between reproductive behavior and other behaviors of the megapodes. Chapters 5–8 discuss aspects of the breeding biology of megapodes including adaptations in embryo physiology and mating strategies. Chapter nine discusses the grim problems associated with island living, habitat destruction, and production of large, nutritious eggs in areas overpopulated with humans—particularly in the context of the breakdown in traditional tribal constraints on over-exploitation of megapode eggs.

The species accounts are thorough, starting with nomenclature and descriptions of plumages, weights and measurements which often include tabular data, range and range maps, previously unpublished sonagrams to augment vocalization descriptions, behavior and abbreviated references (with full references in the References section). I found the abbreviated reference section at the end of each species account, although redundant, an excellent feature since it facilitates looking up references for a particular species. The range maps are excellent, and demarcate ranges of subspecies but many contain historical data and hence do not represent current distribution. For some, however, historical information is identified, and for the Malleefowl *Leipoa ocellata* present and past distributions are given. The plates are excellent, depicting immature plumages and chicks where appropriate, and female plumages in the few dimorphic species. The plates are accompanied by a mini text which is very helpful when perusing or comparing species.

This is a thorough treatment of a fascinating family of birds. The list of more than 800 references, many of them from the 1980s and 1990s, a period of renewed interest and intense research on megapodes, includes references from a wide variety of journals in several languages. Aside from my quibbles about the name changes mentioned above, my only criticism of the book is the level of redundancy, perhaps inevitable in a multi-authored, complicated monograph. We read, for example, that the heat in megapode mounds results from microbial respiration in at least four places. Nevertheless, this is an excellent monograph, the product of exhaustive research, that should be in the library of anyone interest in Australasian birds or in the range of adaptation in birds.—William E. Davis, Jr.

Wilson Bull., 108(4), 1996, pp. 813–824

PROCEEDINGS OF THE SEVENTY-SEVENTH ANNUAL MEETING

JOHN A. SMALLWOOD, SECRETARY

The Seventy-seventh annual meeting of the Wilson Ornithological Society was held Thursday, 11 April, through Sunday, 14 April, 1996 at the Grand Hotel, Cape May, New Jersey, in joint session with the New Jersey Audubon Society. The local committee, chaired by Sheila Lego, was composed of Joan Walsh, Pete Dunne, Tom Parons, Kathy Iozzo, Vince Elia, Bill Seng, Pat Sutton, Marleen Murgitroyde, Fred Mears, Bill Glaser, and Louise Zemaitis. The meeting was sponsored by the Cape May Bird Observatory, New Jersey Audubon Society.

The Council met from 13:17 to 19:02 on Thursday, 11 April in the Grand Ballroom of the Grand Hotel. At that time there were 128 registrants. On Thursday evening there was an informal reception for the conferees and guests at Blackbeard's, a libatory and culinary establishment in the Grand Hotel.

The opening session on Friday convened in the Grand Ballroom at 8:30 with welcoming remarks from Joan Walsh of the Cape May Bird Observatory, New Jersey Audubon Society, and from WOS president Keith Bildstein.

The scientific program included 53 contributed papers and 15 contributed posters, which were organized into four paper sessions, two poster sessions, a symposium on Raptor Migration and Ecology chaired by John C. Kricher, and a workshop on Teaching Ornithology, organized by Edward H. Burtt. The workshop also included field demonstrations on recording bird song and on censusing birds. The evening program on Friday featured Pete Dunne, director of Cape May Bird Observatory, who delivered a well-received presentation entitled "Small-headed Flycatcher. Seen Yesterday. Didn't Leave His Name." This presentation was followed by the first business meeting of the Wilson Ornithological Society, which in turn was followed by another informal reception for members and guests at the above-mentioned Blackbeard's. Field trips on Friday, Saturday, and Sunday morning included forays to Higbee Beach and to other local birding hot spots, and the extended field trip on Sunday included a boat cruise to Back Bay.

The attendees enjoyed a ninety-minute social gathering prior to the annual banquet, which was held in the Grand Ballroom of the Grand Hotel. After a grand dinner, President Bildstein delivered a few brief remarks to the Society. The following awards also were presented:

EDWARDS PRIZE (for the best major article in volume 107 of *The Wilson Bulletin*)

Mary H. Clench and John R. Mathias, "The avian cecum: a review." Wilson Bull., 107 (1):93–121.

LOUIS AGASSIZ FUERTES AWARD

Paul M. Nealen, "Design and function of the Carolina Wren (*Thryothorus ludovicianus*) song system."

MARGARET MORSE NICE AWARD

Susan R. Blackshaw, "A study of wintering Loggerhead Shrikes (*Lanius ludovicianus*) in Texas and/or Florida."

PAUL A. STEWART AWARDS

Paul Doherty, "Avian responses to forest fragmentation: determining the economic cost of maintaining minimum viable populations."

Andrew Dolby, "Benefits of mixed-species flocking for Downy Woodpeckers and White-breasted Nuthatches: a removal experiment."

Kimberley J. Fernie, "Effects of electromagnetic fields generated by powerlines on avian reproduction and development."

Joseph J. Nocera, "The effects of predation on the movement of Common Terns (*Sterna hirundo*) and Arctic Terns (*Sterna paradisaea*) in Nova Scotia."

Elana V. Pravosudova, "The effect of forest fragmentation on social structure of the Tufted Titmouse, *Parus bicolor* (Paridae, Aves)."

ROGER TORY PETERSON TRAVEL AWARD

Sara Morris, "Fall songbird migration in Maine: factors affecting the likelihood of stop-over."

David J. Ziolkowski, Jr., "Coordination of female nest attentiveness with male song output in the House Wren."

ALEXANDER WILSON PRIZE (for best student paper)

Sara Morris, "Fall songbird migration in Maine: factors affecting the likelihood of stop-over."

Selection committee for the Edwards Prize–Charles Blem (chair), Tom Haggerty, Bret Whitney, and Ted Davis; for the Fuertes, Nice, and Stewart Awards–Daniel Klem, Jr., chair, Judith M. Rhymer, and Richard B. Stiehl; for the Peterson Travel Award–John Kricher, chair, Keith Bildstein, and Ted Davis.

Following the award presentations, the guest speaker, Helen Hayes of the American Museum of Natural History, gave a wonderful slide presentation titled "Desperately Seeking Roseates."

FIRST BUSINESS MEETING

The first business meeting was called to order by President Bildstein at 20:35 on Friday, 12 April, in the Grand Ballroom. Secretary Smallwood presented a synopsis of Thursday's Council meeting, and introduced First Vice President Edward H. Burtt, Jr., who discussed his proposal to establish a lectureship for the annual meetings in honor of Margaret Morse Nice. Vice President Burtt suggested the presentation could be an opening plenary lecture or one scheduled at another prominent place in the program. This lectureship would provide the honorary guest speaker a longer format in which to describe scientific inquiry within the overall context of a lifetime of research and personal experience. Secretary Smallwood continued, describing the Council's interest in encouraging high-quality abstracts from Latin America to compete for the Wilson Ornithological Society awards. Because many of these abstracts are written by authors not fluent in English, Jon Barlow generously pledged to oversee those translations. The Council approved a motion to allow the editor to select a recipient of a new award to recognize meritorious service to those who contribute to publishing *The Wilson Bulletin*. Through the efforts of webmeister Janet Hinshaw, the Wilson Ornithological Society now has a home page on the Internet. As of 15 March, 1996, membership in the WOS stood at 2487, including 512 life members. The Council reelected Editor Blem for another term, and expressed its great appreciation. The Council also thanked Ernest

J. Willoughby and the Undergraduate Outreach Committee for its work on teaching ornithology (see the report and committee members, below). In response to the invitation by Jerome A. Jackson, the WOS Council approved a motion to join and send delegates to the North American Banding Council, whose purpose is to facilitate an increase in the quality of data submitted to the Bird Banding Laboratory. No resolutions were received by the retiring Resolutions Committee during the previous year, and a new Resolutions Committee shall be appointed by President Bildstein. Next year's meeting will be hosted by the Division of Biology at Kansas State University from 17–20 April, 1997, in Manhattan, at the invitation of local chair John L. Zimmerman. The 1998 annual meeting will be held in St. Louis from 24–29 March, hosted by the University of Missouri College at St. Louis, with Bette Loiselle the local chair. Although not yet finalized, this is being planned as a joint meeting with the American Ornithologists' Union, the Cooper Ornithological Society, and possibly the Raptor Research Foundation and the Colonial Waterbird Society. Council gratefully accepted the invitation from local chair Herbert T. Hendrickson to host the 1999 annual meeting at the University of North Carolina at Greensboro. The secretary then asked those assembled to stand in recognition of the following members who have died since we last met: Andrew J. Berger (Kailua, HI), Mrs. W. P. Cottrile (Jackson, MI), John Farrand, Jr. (Summit, NJ), James M. Hartshorne (Ithaca, NY), Thomas A. Imhof (Birmingham, AL), Herbert W. Kale (Casselberry, FL), C. N. Mason (Washington, DC), Robert A. McCabe (Madison, WI), John T. Ricks (Huntington, NY), Carol S. Roesler (Darien, CT), Walter Spofford (Portal, AZ), Gustav A. Swanson (Ft. Collins, CO), Arthur C. Taylor (Appleton, WI), and Gerard F. Van Tets (Lyneham, Australia).

The treasurer's report was then presented by Doris Watt.

Charles Blem presented the editor's report.

William (Ted) Davis, chair, presented the report of the nominating committee, which also included Mary H. Clench and Jerome A. Jackson: President, Keith L. Bildstein; First Vice-president, Edward H. Burtt, Jr.; Second Vice-president, John C. Kricher; Secretary, John A. Smallwood; Treasurer, Doris J. Watt; Members of Council for 1997-1999, Peter C. Frederick and Danny J. Ingold.

Vice-president Burtt introduced members to the newly formed Mesoamerican Society for Biology and Conservation, which will publish a news bulletin and sponsor annual conferences in Mesoamerica.

The meeting was adjourned at 20:58.

SECOND BUSINESS MEETING

The second business meeting was called to order by President Bildstein at 11:07 on Saturday, 13 April, in Room 127 of the Grand Hotel, at which time he asked Secretary Smallwood to read aloud the single resolution to be considered:

COMMENDATION

WHEREAS the Wilson Ornithological Society held its annual meeting in scenic Cape May, New Jersey, at the invitation of the New Jersey Audubon Society,

RECOGNIZING that the Committee on the Scientific Program, under the adept direction of John C. Kricher, arranged and managed an exemplary schedule of oral and poster presentations, which included an innovative workshop on teaching ornithology, organized by Edward H. Burtt, Jr., and

RECOGNIZING that the Committee on Local Arrangements, through the efforts of Sheila Lego, Joan Walsh, and other members of the New Jersey Audubon Society's Cape May Bird Observatory, provided an excellent conference venue with comfortable accommoda-

tions, interesting guest speakers of national renown, exciting bird watching opportunities, and, through mechanisms not yet revealed, outstanding local weather, and

WHEREAS the conferees found this meeting informative and enjoyable,

THEREFORE BE IT RESOLVED that the Wilson Ornithological Society commend the Committee on the Scientific Program, the Committee on Local Arrangements, and the local sponsors for a most successful and rewarding meeting in Cape May.

The motion to accept this resolution was made by Herbert T. Hendrickson, seconded by Clait Braun, and enthusiastically passed by acclamation.

The President recalled the report of the Nominating Committee to the floor, asking for any additional nominations. As there were none, Phillips B. Street moved and Clait Braun seconded that the nominations be closed, and, by acclamation, it was so. Further, Herbert T. Hendrickson moved and Richard N. Conner seconded that the candidates for all offices be elected unanimously, and again by acclamation, this too came to pass.

The President invited David Blockstein, chairman of the Ornithological Council, to address the members assembled. Dr. Blockstein reviewed the issues of current interest to the Ornithological Council, including improvements to the process of issuing federal scientific permits, the relocation of the National Biological Service (which administers the Bird Banding Laboratory) into the United States Geologic Survey, reauthorization of the Endangered Species Act, and a revision of the guidelines on the research use of wild birds.

The members in attendance were treated to a slide show by John Zimmerman that previewed the beautiful Kansan scenes we would behold next year at the 1997 WOS meeting in Manhattan. This meeting will be the initial site for the Nice Lecture, and a symposium on grassland birds is being planned. President Bildstein presented an update on the plans to meet in St. Louis, Missouri, in 1998, and in Greensboro, North Carolina, in 1999.

President Bildstein then called on those assembled for any announcements, but none were offered. Adjournment occurred at 11:32.

REPORT OF THE TREASURER
1 July 1995 to 30 June 1996

GENERAL FUNDS

Balance Forward		$ 89,713.18
Receipts		
Regular and Sustaining Memberships	$ 33,226.00	
Student Memberships	4,505.00	
Family Memberships	176.00	
Total Dues		$ 37,907.00
Subscriptions	$ 25,919.16	
Contributions from Authors for Page Charges	9,549.26	
Back Issues	664.00	
Total Income from the Publications		$ 36,132.42
Contributions to The Van Tyne Library	$ 355.00	
Contributions to the Student Membership Endowment	0.00	
Contributions to the Wilson Award Endowment	0.00	
Contributions to the General Endowment (Life, Patrons)	375.00	
Contributions to the Roger Tory Peterson Travel Fund	0.00	
Contributions to the General Endowment	498.00	
Unrestricted Contributions	458.00	

Total Contributions		$ 1,686.00
Royalties		42.00
Interest from Endowments		24,820.25
Interest from Checking Account		540.73
Dividends from Dreyfus Account (Reinvested)		841.80
List Rental		1,034.00
Miscellaneous		1,313.09
OSNA Adjustment		−587.99
TOTAL RECEIPTS		$103,729.30
Disbursements		
Bulletin Publication		
June 1995	$ 19,464.22	
September 1995	16,904.22	
December 1995	22,141.22	
March 1996	19,397.82	
Editor's expenses	5,168.29	
Total Publication Costs		$ 83,075.77
OSNA Expenses	$ 13,948.00	
Secretary's Expenses	79.50	
Treasurer's Expenses	81.63	
Treasurer's Bond	0.00	
The Flock	259.52	
Editor's Honorarium	2,000.00	
Incorporation Fee	5.00	
Awards Committee Phone	66.75	
Meeting Costs/Symposium Speakers' Airfare	2,148.10	
Advertisement (Allen Press)	0.00	
CPA (Tax Filing)	425.00	
Van Tyne Library (Back Issues)	40.00	
AAZN Dues	100.00	
Miscellaneous (Western Union, Refunded Later)	850.00	
Total Operating Expenses		$ 20,003.52
Organizational Awards	$ 2,206.00	
Ornithological Council Contribution	500.00	
Total Philanthropies		$ 2,706.00
TOTAL DISBURSEMENTS		$105,785.29
Transfer to Mellon Account		$ 22,813.00
Ending Balance		$ 64,844.19

CASH ACCOUNTS

First Source Bank Checking Account 1 April 1996	$ 45,408.95	
Dreyfus Liquid Assets 1 March 1996	19,435.24	
Total Cash on Hand		$ 64,844.19
Van Tyne Library Accounts Starting Balance	$ 2,857.19	
Receipts	$ 1,171.10	
Expenses	1,123.42	
Ending Balance		$ 2,904.87

DESIGNATED ACCOUNTS

Sutton Color Plate Fund (Endowment Principal $55,727.99)	
1995 Balance	$ 500.20
1995 Earnings[1]	$ 2,173.39
Funds Disbursed for Color Plates 1995–96	2,654.00
1996 Balance	19.59

TOTAL ENDOWMENT FUNDS

1989 Market Value	$386,992.00
1990 Market Value	$372,063.00
1991 Market Value	$423,698.00
1992 Market Value	$430,258.00
1993 Market Value	$487,786.00
1994 Market Value	$425,155.00
1995 Market Value (June 1995)	$555,600.00
1996 Market Value (March 1996)	$647,600.00

[1] Based on 3.9% interest on Mellon account.

EDITOR'S REPORT—1995

In 1995, 213 manuscripts (112 major papers, 101 short communications) were received by the *Wilson Bulletin* 1editorial office. This is 32 more than in 1994. Of these, approximately 61% were rejected. The time between receipt of manuscript from the author(s) and our return of the manuscript with referee comments nearly always has been less than three months. A few manuscripts required slightly more than four months for a decision. There is a modest backlog of manuscripts, because we have reset deadlines one month earlier. The average time between receipt of a manuscript and its appearance in *The Wilson Bulletin* in 1995 was almost always less than a year, as in past issues. Frontispiece articles sometimes require longer to appear in print, depending upon backlog of such papers. We are using e-mail in the editorial process to the degree that some costs have been reduced and the speed of response for computer users often is more prompt.

1 am grateful to the editorial board—Kathy G. Beal, R. N. Conner, Tom Haggerty, and J. A. Smallwood—for their timely, skilled evaluations of many of the manuscripts submitted to the journal. Assistant Editors Leann Blem and Albert E. Conway are responsible for the consistency of style and format, and for making arcane prose more readable. I thank them for their efforts. Kathy G. Beal deserves special praise for continuing to assemble the index for *The Wilson Bulletin.* This is a tedious task and the entire society benefits from her careful work. Leann Blem has provided much of the manual labor that keeps the editorial office running and she catches many of the small errors that can plague a publication. Virginia Commonwealth University Departmcnt of Biology supports the editorial process and the running of the office in numerous ways. As always, I remain open to suggestions as how to improve the service we provide the readers and authors, and invite you to make your opinions known to me.

C. R. Blem, *Editor*

The reports of the standing committees are as follows:

REPORT OF THE MEMBERSHIP COMMITTEE

The current members of the WOS membership committee are Jim Ingold at Louisiana State University, Mark Woodrey at the Mississippi Museum of Natural Science, Mary Clench at the University of Texas, and myself, at Montclair State University in New Jersey.

Mary Clench joined the committee in 1995, offering to contact nonrenewing members to invite them back into our flock. This proved to be a formidable task: about 350 members did not renew in 1995, and about 280 in 1994. Mary has been concentrating on the most recent drop-outs. Mark Woodrey continues to send membership invitations to authors who publish in The Wilson Bulletin, and Jim Ingold contacts nonmembers who make presentations at the annual meetings.

Dave Cimprich, who formerly oversaw the itinerary of the WOS membership poster, has retired. During the past year I brought the poster to the WOS meeting in Williamsburg, the Raptor Research meeting in Duluth, and the AOU meeting in Cincinnati. I'm not sure how effective of a recruitment device the poster has been at OSNA-member societal meetings, where a large percentage of the participants already are familiar with the WOS. The poster may have a greater impact at regional gatherings, and at meetings of highly motivated bird-people, such as members of Audubon and the American Birding Association. I am currently seeking a new membership committee person who will have the time and energy to implement an aggressive traveling schedule for the poster. Suggestions will be appreciated.

I received during the past year 14 letters from people interested in joining us. I sent to each a personal letter of welcome and our membership brochure. I recently revised the brochure; the editorial suggestions forwarded to me by Janet Hinshaw were particularly helpful. Both the scanned artwork and the brochure's layout are incorporated into a WordPerfect© document, so that laser printing produces a camera-ready copy, and future edits may be made easily. At this writing the new brochures are at the printers. I plan to bring a supply of them to Cape May.

John A. Smallwood, *Chair*

REPORT OF THE UNDERGRADUATE OUTREACH COMMITTEE

The Committee on Undergraduate Outreach was established in June, 1991, under President Richard C. Banks, to help stimulate an interest in ornithology among undergraduate students, and to help maintain and focus that interest so as to stimulate students to continue studies in ornithology. The Committee has explored ways to increase interest of undergraduate students in ornithology both as a focus for future postgraduate studies, and as an avocation for those who seek careers in fields other than biological sciences.

Members of the Committee during 1995–1996 were (alphabetically): Albert R. (Jay) Buckelew, Jr., Bethany College, WV; Edward H. Burtt, Jr., Ohio Wesleyan University, OH; Danny J. Ingold, Muskingum College, OH; Dale Kennedy, Albion College, MI; John C. Kricher, Wheaton College, MA; Lynn A. Mahaffy, Randolph-Macon College, VA; Barnaby Marsh IV, Cornell University, NY; Dan A. Tallman, Northern State University, SD; Ernest J. Willoughby, St. Mary's College of Maryland; W. Herbert Wilson, Colby College, ME. Of these members, Buckelew was appointed to the Committee by President Keith Bildstein in October, and Ingold resigned in February.

The Committee has completed its analysis of the returns on its questionnaire distributed to teachers of college undergraduates in November, 1993, for the purpose of helping us to decide what to do to promote education in ornithology. A copy of the complete analysis has been submitted to the secretary. The Committee will be discussing these results in its sessions at the annual meeting.

The Committee decided last year to organize an ornithology teaching workshop for this year's annual meeting. Dr. Burtt and Dr. Kricher took charge of organizing and scheduling that workshop in the program.

Work on the Committee's guide to graduate degree programs in ornithology continues. The process of organizing and keyboarding the information from many institutions that responded to our request has taken longer than we supposed it would. At the same time, the Committee has received several requests for copies when they become available.

Dan Tallman continues to supervise our electronic information exchange.

The Committee is working on a project to produce a series of videotape interviews with eminent ornithologists. Such tapes could be lent through the WOS library. Lynn Mahaffy is chairing a subcommittee to draft a series of questions for such interviews.

Ernest J. Willoughby, *Chair*

REPORT OF THE JOSSELYN VAN TYNE MEMORIAL LIBRARY COMMITTEE

Once again at year's end, thanks in large part to the constant hard work of Janet Hinshaw and her helpers (operating from the Bird Division Library, University of Michigan Museum of Zoology, our WOS Library's "home base"), we can report satisfactory progress and many worthwhile services, both to our membership and to the science of ornithology. Our special thanks again to Pat Ahrens, secretary for the Bird Division.

Donations to the library during the year included 30 books, 57 reprints, 241 journal issues, 19 reports, and two microfilm dissertations; the reprints and journal issues, for whatever reasons, show a sharp drop-off from last year. The number of members and institutions contributing, however, remained about the same, 23, namely: S. Conant, S. Emslie, A. Feduccia, A. Gaunt, S. Goodman, G. Hall (*The Wilson Bulletin* review copies), J. Hinshaw, J. Jackson, L. Kiff (for The Peregrine Fund), N. Klein, S. Latta, F. Lohrer, P. Lowther, H. Mayfield, H. McClure, R. Payne, D. Pence, T. Root, J. Ryder, C. Shipman, J. Spendelow, Station Ornithologique Suisse, and P. Street. One can't help noting, after many years, the absence of the late Andy Berger's name as a leading donor.

Gifts to other institutions were as follows: 32 journal issues to Grand Valley State University, 52 journal issues to Hawk Mountain Sanctuary, 128 journal issues to The Peregrine Fund, four journal issues to Station Ornithologique Suisse, and 83 journal issues to the Zoological Museum, University of Moscow.

Loan transactions totaled 98, to 60 people, the almost twofold increase being partly due to our providing copies to various individuals working on *Birds of North America* accounts—certainly justifiable even if our rules had to be relaxed a bit.

The total of publications regularly received in our library, 290 titles from 199 organizations, comprise the following: 127 exchanges (192 journals, books, and reprints), 51 gifts (67 publications), and 21 subscriptions (31 titles). These figures show a continuing upward trend.

During the year, we sold 52 books for $2535.05 ($1022 in cash; $1513.05 in trade for credit with Buteo Books), and 72 journal issues for $132.00: a total of $2677.05. These items are from the accumulating backlog of member contributions which, though surplus duplicates, have a very large cash value.

This cash accrues to replenish our New Book Fund. In this past year, a total of $1414.55 was spent from this fund: $701.38 for 36 books, monographs, tapes, and records; $292.17 for back issues of journals; and $421.00 for 12 journal subscriptions. Such purchases are adding very substantially to the overall value of our holdings.

One could hardly look at our figures and not be very much encouraged by the general picture. All we can do is once more thank the many who have been involved, while urging more members to use our library and to contribute what they can to its support.

We would encourage everyone to view our web page, which can be found at http://www.ummz.lsa.umich.edu/birds/wos.html. There is a link to the University of Michigan's on-line library catalogue (MIRLYN) which provides listings of the catalogued books and journals in the Van Tyne library.

William A. Lunk, *Chair*

PAPER SESSIONS

Richard C. Banks, National Biological Service, National Museum of Natural History, Washington, DC, "The name of the Lawrence's Flycatcher."

Jon C. Barlow and G. Cooke, Dept. of Ornithology, Royal Ontario Museum, Toronto, ON, Canada, "Variation in song in circum-Caribbean peppershrikes: subspecies identity of the Isla Margarita population."

Mark Fink, Dept. of Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, TX, "Effect of edge on nest predation within Golden-cheeked Warbler habitat."

Jeanette Bider, Univ. of Arkansas, Fayetteville, AR, "Use of microhabitats by woodcreepers (Dendrocolaptidae) and flycatchers (Tyrannidae) in tropical broadleaf forest remnants."

C. T. Baril, Dept. of Zoology, Univ of Toronto, and Dept. of Ornithology, Royal Ontario Museum, Toronto, ON, Canada, "Geographic variation in *Vireo huttoni* territorial song."

Leonard Reitsma, Benjamin Steele, Sherman Burson, and Peter Hunt, New England Institute for Landscape Ecology, "Habitat selection and socioecology of Louisiana (*Seiurus motacilla*) and Northern Waterthrushes (*S. novaboracensis*) overwintering in Puerto Rico, West Indies."

Daniel S. McGeen, Auburn Hills, MI, "Atoms, ions, and the warbler."

J. M. Utter, B. Farrell, F. Arengo, R. Drummond, C. Lindner, C. Smith, and C. Safina, Purchase College, SUNY, Purchase, NY, "Overwinter decline in multiflora rose fruit on mockingbird territories."

Eric C. Atkinson, Hawk Mountain Sanctuary Association, Kempton, PA, Pam Dugger and Christina Swindall, Boise State Univ., Boise, ID, "Year-round habitat association of Black-billed Magpies, Horned Larks, and Western Meadowlarks on the Snake River Birds of Prey National Conservation Area."

Barbara J. Bowen, Dept. of Biology, Central Connecticut State Univ., New Britain, CT, "Comparisons of predation rates on artificial and natural avian nests in open, edge, and forested habitats."

Catherine M. Devlin, Rutgers Univ., New Brunswick, NJ, "The Eastern Wild Turkey (*Meleagris gallopavo silvestris*) in the southern pinelands of New Jersey."

Winli Lin, Univ. of San Diego, San Diego, CA, "Parental behavior and possible brood division in Whimbrel (*Numenius phaeopus*)."

Sylvia L. Halkin, Dept. of Biological Sciences, Central Connecticut State Univ., New Britain, CT, "Recording and analysis of bird vocalizations."

W. Herbert Wilson, Colby College, Waterville, ME, "Teaching the fundamentals of bird vocalizations: a laboratory on computer-aided analysis."

Alex Dowling, Dept. of Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, TX, "Impacts of habitat fragmentation on Prothonotary Warblers in east Texas."

Mark R. Ryan, School of Natural Resources, Univ. of Missouri, Columbia, MO, "Teaching optimal foraging behavior: an experiment on group vs. solitary foraging."

Ernest J. Willoughby, St. Mary's College of Maryland, St. Mary's City, MD, "Field study of migratory behavior."

Edward H. Burtt, Jr., Dept. of Zoology, Ohio Wesleyan Univ., Delaware, OH, "Teaching identification of birds through censusing habitats that differ in the extent of human impact."

Doris J. Watt, Biology Dept., Saint Mary's College, Notre Dame, IN, "A laboratory exercise in armchair biology."

Bruce G. Peterjohn, John R. Sauer, and William A. Link, National Biological Service, Patuxent Wildlife Research Center, Laurel, MD, "Mapping change in bird distributions from breeding bird survey data."

John R. Sauer, William A. Link, and Bruce G. Peterjohn, National Biological Service, Patuxent Wildlife Research Center, Laurel, MD, "Estimating population change from the North American Breeding Bird Survey."

Andrew B. T. Smith, Univ. of Ontario, ON, Canada, "Changes in the abundance of forest birds in Algonquin Park: 1952–1995."

Kurtis L. Dean and David L. Swanson, Univ of South Dakota, Vermillion, SD, "Seasonal variation in density and diversity of neotropical migrants at stopover sites in the northern great plains."

Deanna K. Dawson, Patuxent Wildlife Research Center, Laurel, MD, and Lonnie J. Darr, Montgomery County Dept. of Environmental Protection, Rockville, MD, "Land-use planning for area-sensitive forest birds."

Eric T. Liknes, Kurtis L. Dean, and David L. Swanson, Dept. of Biology, Univ. of South Dakota, Vermillion, SD, "Differential timing of migration of sex/age classes in Ruby-crowned Kinglets."

Joseph R. Jehl, Jr., Hubbs-Sea World Research Institute, San Diego, CA, "Leaving town: how Eared Grebes prepare to migrate."

Ronnie E. Stout, North Dakota State Univ., Fargo, ND, "Fall Red-necked Grebe migration behavior and molt in the Great Lakes region."

Chao-Chieh Chen and R. B. Hamilton, Louisiana State Univ., Baton Rouge, LA, "Analysis of searching movements of insectivorous migratory songbirds on the Chenier Plain of the Gulf Coast."

Sara R. Morris, Cornell Univ., Ithaca, NY, "Fall songbird migration in Maine: factors affecting the likelihood of stopover."

Jeffrey P. Dugay and Petra S. Wood, West Virginia Cooperative Fish and Wildlife Research Unit, NBS, West Virginia Univ., Morgantown, WV, "The management effects of clearcuts and two-age timber harvests on nongame birds in West Virginia."

John A. Smallwood, Dept. of Biology, Montclair State Univ., Upper Montclair, NJ, and Peter D. Smallwood, Dept. of Biology, Univ. of Pennsylvania, Philadelphia, PA, "Decoy holes and monitoring rates: applied conservation biology for secondary cavity nesting species."

Bradley D. Ross and Richard H. Yahner, Dept. of Ecology, Pennsylvania State Univ., University Park, PA, "Integrating habitat and bird variables using geographic information systems and extensive wildlife data sets."

Bruce W. Baker, Brian S. Cade, Warren L. Mangus, National Biological Service, Fort Collins, CO, Janet L. McMillen, Dept. of Zoology, Ohio State Univ., Columbus, OH, and F. Joshua Dein, National Biological Service, Madison, WI, "Multi-scale evaluation of a suitability model for Sandhill Crane nesting habitat."

Robert W. Russell, National Oceanographic and Atmospheric Association, Seattle, WA, "Boundary-layer convergence lines: aerial corridors for soaring birds."

B. G. Murray, Jr., Dept. of Biological Sciences, Rutgers Univ., Piscataway, NJ, "On the meaning of 'reproductive success' and other terms."

Peter W. C. Paton, Univ. of Rhode Island, Kingston, RI, and Ron Flores, U.S. Fish and Wildlife Service, Ninigret NWR, Charlestown, RI, "Effects of the North Cape barge oil spill on the distribution of birds in coastal Rhode Island."

Richard N. Conner, D. Craig Rudolph, Southern Research Station, U.S. Forest Service, Nacogdoches, TX, and Robert N. Coulson, Dept. of Entomology, Texas A&M Univ., College Station, TX, "Relationships between southern pine beetle population level and bark-beetle caused mortality of Red-cockaded Woodpecker cavity trees."

D. Craig Rudolph and Richard N. Conner, Southern Research Station, U.S. Forest Service, Nacogdoches, TX, "Red-cockaded Woodpeckers, ecosystem management, and silviculture."

Douglas W. White, Albion College, Albion, MI, "Effect of egg burial on nest vandalism by House Wrens."

L. Scott Johnson, David Ziolkowski, Dept. of Biology, Towson State Univ., Towson, MD, Krishna Hannam, and William A. Searcy, Dept. of Biology, Univ. of Miami, Miami, FL, "Coordination of female nest attentiveness with male song output in the House Wren."

E. Dale Kennedy and Douglas W. White, Albion College, Albion, MI, "Competition between Bewicks Wrens and House Wrens."

Gregory S. Keller, School of Forest Resources, Pennsylvania State Univ., University Park, PA, "Seasonal distribution and community composition of avifauna in isolated deciduous forest patches."

Ernest J. Willoughby and Christopher J. Lindsay, St. Mary's College of Maryland, St. Mary's City, MD, "Significance of the odd prenuptial molt of American Goldfinch."

Todd J. Underwood and Roland R. Roth, Dept. of Entomology and Applied Ecology, Univ. of Delaware, Newark, DE, "Estimating Wood Thrush population demographics by constant effort mistnetting."

Jake Stein, Univ. of Tennessee at Martin, Martin, TN, "Effects of sex, time of day, and age on Carolina Chickadee weights."

David M. Whalen, Center for Conservation Biology, College of William & Mary, Williamsburg, VA, "Fall migration of Northern Saw-whet Owls at the southern tip of the Delmarva Peninsula."

Keith L. Bildstein and Laurie J. Goodrich, Hawk Mountain Sanctuary, Kempton, PA, "Linking raptor migration watch-site counts to mainstream ecology and conservation: 60 years of science at Hawk Mountain Sanctuary."

Paul Kerlinger, New York, NY, "Economics of hawk watching."

David F. Brinker, Maryland Dept. of Natural Resources, Annapolis, MD, "Migratory movements of Northern Saw-whet Owls: what do we really know?"

Jacques Ibarzabal, École de la mer des Jeunes Explos., Beauport, PQ, Canada, and Jean-Pierre L. Savard, Canadian Wildlife Service, Sainte-Foy, PQ, Canada, "Migration monitoring in Tadoussac, Quebec."

Robert W. Russell, National Oceanic and Atmospheric Administration, Seattle, WA, "Water-crossing tactics of migrating hawks at Cape May Point."

Richard P. Gerhardt, Miguel Angel Vasquez, and Paula M. Harris, The Peregrine Fund, Inc., Boise, ID, "Observations and food habits of nesting Great Black Hawks in El Peten, Guatemala."

POSTERS

J. A. Dick, R. D. James, and J. C. Barlow, Dept. of Ornithology, Royal Ontario Museum, Toronto, ON, Canada, "Current status of transient Rufous Hummingbirds in Ontario."

Alix Dowling, Dept. of Wildlife and Fisheries Sciences, Texas A&M Univ., College Station, TX, "Impacts of habitat fragmentation on Prothonotary Warblers in East Texas."

Jessica R. Eberhard, Princeton Univ., Princeton, NJ, "The evolution of nest-building in parrots."

H. T. Hendrickson, Univ. of North Carolina at Greensboro, Greensboro, NC, "History of winter populations of Purple Finch in eastern North America."

Peter Hunt, Mascoma Lake Bird Observatory, Enfield, NH, "Winter distribution of the sex and age classes of the Yellow-rumped Warbler."

Michael J. Justice, Dept. of Psychology, Dominican College, Orangeburg, NY, and Teresa C. Justice, Dept. of Psychology, Iona College, New Rochelle, NY, "Random mating by size in Northern Mockingbirds."

T. Greg King, Mark A. Howell, Brian R. Chapman, Karl V. Miller, and Sandra S. Chapman, School of Forest Resources, Univ. of Georgia, Athens, GA, "The effects of growing-season vs. dormant-season prescribed fire on neotropical migrant birds."

Brook Lauro, St. John's Univ., Jamaica, NY, "The foraging ecology of Sooty Oystercatchers (*Haematopus fuliginosus*) nesting at rocky shores in Australia."

Lynn A. Mahaffy and Kendall Malone, Randolph-Macon College, Ashland, VA, "Some effects of mosquito control on submerged aquatic vegetation utilized by waterfowl."

R. McLain, Dept. of Entomology and Applied Ecology, M. Parcells, Dept. of Animal and Food Sciences, and R. Roth, Dept. of Entomology and Applied Ecology, Univ. of Delaware, Newark, DE, "Determining sex of Wood Thrush by flow cytometry."

John O'Reilly and Roland R. Roth, Univ. of Delaware, Newark, DE, "Within-season changes in nest location and mate by female Wood Thrushes."

Jeanette Rilling, Frederick Terranova, and Terry L. Master, East Stroudsburg Univ., East Stroudsburg, PA, "Habitat selection and population status of the Louisiana Waterthrush (*Seiurus motacilla*) in the Delaware Water Gap National Recreation Area."

Michel Robert and Pierre Laport, Canadian Wildlife Service, Sainte-Foy, PQ, Canada, "Yellow Rail distribution, habitat and conservation along the St. Lawrence River, southern Quebec."

James A. Sedgwick, National Biological Service, Fort Collins, CO, "Some aspects of Willow Flycatcher population dynamics."

Jeffrey A. Spendelow, Patuxent Environmental Science Center, NBS, Laurel, MD, James M. Zingo, Massachusetts Cooperative Fish and Wildlife Research Unit, NBS, Univ. of Massachusetts, Amherst, MA, David A. Shealer, Dept. of Biology, Rutgers Univ., Piscataway, NJ, and Grey W. Pendleton, Patuxent Environmental Science Center, NBS, Laurel, MD, "Growth and fledging of Roseate Terns in exceptionally 'good' and 'poor' years of overall productivity."

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By Kathleen G. Beal

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This issue of *The Wilson Bulletin* was published on 31 December 1996.

The Wilson Bulletin

PUBLISHED BY THE WILSON ORNITHOLOGICAL SOCIETY

VOLUME 108 1996 QUARTERLY

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The Wilson Bulletin

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